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W. G. FARLOW

Dr. W. G. Farlow
with the sincerest regards of
George J. Peirce

A TEXT-BOOK

OF

PLANT PHYSIOLOGY

BY

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PREFACE

The course in Plant Physiology which I have given for the last five years at Stanford University has impressed upon me the need of a text-book which treats the subject less exhaustively than Pfeffer's Handbuch and more fully than Noll's section of the Bonn text-book.* As I did not know of such a book in any language, I began to write my lectures. These lectures, after repeated working over, have finally taken this definite form.

My intention has been to present the main facts of plant-physiology and the saner hypotheses regarding them, striving to express safe views rather than to echo the most recent, attempting here and there to suggest definite problems for investigation, and everywhere trying to avoid giving the impression that the science or any part of it has reached ultimate knowledge and final conclusions.

I have purposely made no attempt to give directions for experiments, believing that a laboratory manual and a text-book must meet such different needs that the style of the one is impossible for the other. This book must, however, be supplemented by actual laboratory work by the reader, under the guidance of a teacher or of some of the laboratory manuals mentioned on page 27, or both.

No one can work on the physiology of plants nowadays without being conscious of his indebtedness to Pfeffer. If Pfeffer had done nothing else, the preparation of the two editions of his Handbuch, in which the literature of the subject is brought together, and the present status of the science is well set forth, would secure him an honored place. I cannot refrain from acknowledging my personal as well as professional obligation to him, and I do so with the utmost satisfaction.

---

* Lehrbuch der Botanik. Strasburger, Noll, Schenck, Schimper. Five editions. English translation by Porter.

It is also a great pleasure to express my grateful appreciation of the help I have received from my associates in this University, Dr. Anstruther A. Lawson (Botany), Professors Herman De C. Stearns (Physics), Frank M. McFarland (Histology), William A. Cooper (German), and especially from Professor Douglas H. Campbell. I am indebted also in various ways to my friends Professor William F. Ganong of Smith College, and Dr. Hermann von Schrenck of Washington University, St. Louis. Professor Walter R. Shaw of the University of Oklahoma generously allowed me to use his excellent photograph of *Postelsias* reproduced on page 190. Dr. Daniel T. MacDougal of the New York Botanical Garden and his publishers, Messrs. Longmans, Green & Co., have given me permission to use the figures of *Mimosa* on pages 248–9. Professor Goebel of Munich kindly sanctions my use of his figure of *Opuntia* shown on page 210. To these and all others who have assisted me I wish most heartily to express my sincerest thanks.

G. J. P.

Leland Stanford Junior University,
California, December, 1902.

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PLANT PHYSIOLOGY

CHAPTER I

INTRODUCTION

ALL living beings are alike in kind, differing from one another only in degree. To this conclusion scientific men have been gradually driven back by the failure of every attempt to discover and to define any fundamental difference between animals and plants. The differences between the higher representatives of the two so-called kingdoms—animal and vegetable—are so striking that no one can fail to see them. Between the higher and the lower animal forms are differences as striking as those between higher animals and higher plants. Between the higher and lower plant forms there are similar differences. Likenesses always accompany these differences. It is these likenesses which enable us to call a given organism an animal or a plant. Between the higher and lower members of the same kingdom, and between the higher members of the two kingdoms, the differences are so striking that the attention is almost wholly occupied with them. It is natural that we should look more for differences than for likenesses: for our ability to distinguish our friends from our enemies, our own from our neighbor's possessions, the Bird-foot Violet from the Swamp Violet, the dog from the tree, is dependent upon our perception of differences between them. It is necessary that we see differences: the more intelligent the man, the keener is his perception of differences; the higher the organism, the greater is its difference from others.

The study of low organisms reveals few differences. Successfully to study such low organisms as the bacteria demands unusual ability to detect the differences between them. The differences disappear as we descend the scale of development, and the likenesses become more and more evident. The bacteria and diatoms, which have been repeatedly regarded first as animals, then as plants, and the *Myxomycetes* (slime-moulds), which are still believed by some to be animals (*Mycetozoa*), illustrate the difficulty of determining to which "kingdom" these organisms belong. It is important to the students of systematic botany and zoology to know where to place these organisms in their systems of classification. This enables other naturalists to go further. To the physiologist it is a convenience rather than an essential to know whether the organism which he is studying is called an animal or a plant, but the results of his work have often been useful to the systematists in confirming or correcting their classifications. From the classifier's point of view the differences which enable him to make an orderly arrangement of the objects of his study are of the utmost importance; from the physiologist's standpoint the likenesses are most important. This will become plainer when we state the aim of physiology.

THE AIM OF PHYSIOLOGY

According to Pfeffer,* "the aim of physiology is to study the nature of all vital phenomena in such a manner that, by referring them to their immediate causes, and subsequently tracing them to their ultimate origin, we may arrive at a complete knowledge of their importance in the life of the organism." Physiology is a study not merely of structure, though to its successful pursuit a knowledge of structure is indispensable; nor of organized bodies, though a knowledge of the laws which govern their organization (structure and form) is important. It is the study of the living organism. Crystals have definite and characteristic structures and forms, they increase in size and in number in accordance with a few laws common to all and a few laws peculiar to each kind. The carbon compounds have definite structures, as Kekule's demonstration of the benzole-ring proved; they form under certain conditions and their behavior is characteristic of the kind. A machine has definite structure, it operates in a fashion characteristic of its kind. Physiology has long been conceived to be the study of the structure and operations of peculiar machines, the study of functions as based upon a knowledge of anatomy. The physiologist is now striving not only to know the functions which are the manifestations of the life possessed by complicated living structures or organisms, but also to determine the causes both of structure and of functions. In an engine we have a structure which, under certain knowable conditions, does certain kinds of work. The materials and the construction of the engine are lifeless; the engine is the result of human intelligence acting in harmony with physical laws upon lifeless material; the working of the engine is the result of energy (physical force) applied through human intelligence to it; the structure itself and its working are the result of physical forces acting upon inert materials in harmony with physical laws comprehended by the designer and driver of the engine. These are all external to the structure and are consciously taken advantage of and applied to and through the engine by the living organisms concerned in its construction and operation.

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* Handbuch der Pflanzenphysiologie, 2te Auflage, Bd. I., p. 7, 1897. English translation by Ewart, Physiology of Plants, vol. I., p. 8, 1900.

A living organism is a structure existing in harmony with physical forces and laws and because of them. Few living organisms strive to ascertain, and none fully knows, what these forces are. The materials employed in the construction of a living organism are inert, lifeless; they are arranged in harmony with, and through the operation of, physical laws and forces; but the inert materials are acted upon and the physical forces employed by the organism itself, and for the most part unconsciously.

Between the engine and the living organism there is then a radical difference; the engine and the organism, though both machines, differ in that life, external though applied to the one, is internal and possessed by the other. The difference thus stated is one plainly felt but inadequately expressed, for who can tell what **life** is? Just as we say that walking consists in the rapid restoration of the body to a position of equilibrium after falling, so we may say that living consists in the maintenance of the equilibrium between constructive and destructive influences and processes. But living is the evidence of life, just as thinking is the evidence of brain; living is not life itself. However, in studying the means by which the equilibrium between constructive and destructive influences is maintained—the means by which living is attained—we are approaching the eternal question: What is life itself?

In determining that the means of maintaining the equilibrium between constructive and destructive influences are physical and chemical, and that the influences themselves are physical and chemical, not peculiar "vital" forces, not occult or supernatural, one question regarding life is answered. Whatever may be our views regarding the origin of life, there is no scientific or other heresy in accepting the present evidence that life maintains itself, and is maintained, by physical and chemical means only. In the following pages these means will be examined and discussed.

Pfeffer's statement, quoted above, of the aim of physiology does not limit the study to the manifestations of life in either "kingdom" of organisms. One evidence of the wisdom of such a broad view is the value which Pfeffer's own investigations, conducted mainly on plants—particularly perhaps those on osmosis and on irritability—possess for the animal physiologist. When physiologists, not satisfied with the observation and description of the phenomena displayed by the different kinds of living organisms, began to seek for the means by which these phenomena are executed and for their causes, comparison revealed that the causes, the means, and even the phenomena themselves, are alike in all organisms. Physiology is now, therefore, a much broader as well as deeper science than it was formerly conceived to be, and though there are now and always must be animal and plant physiologists, they are studying common problems and contributing to the common mass of human knowledge of living organisms.

It is often a matter of chance or of convenience which determines whether a man shall study one organism or another. Sachs,* who may be called the founder of modern plant-physiology, has said that although plant-physiology owes much to animal-physiology, yet animal-physiology is being enriched by the results attained by plant-physiologists. The appreciation of the fundamental unity of the aims and the results of animal and plant physiologists has recently led to the publication of two books on general physiology.† In such books the manifestations of life are described and discussed in a broad way; for details one must turn to the special treatises on the physiology of animals and plants.

Though the phenomena of life are the same in all organisms, life manifests itself in special ways in different organisms, making some more favorable for the study of special phenomena than others. For example, the manufacture of starch from carbon-dioxide and water, and the formation of tannin and certain other by-products in nutrition, are subjects in plant-physiology only, just as other special functions, such as those of nerves and muscles, carried out by extremely differentiated organs, and the circulation in vessels, are subjects in animal-physiology only. Again, it is more convenient to study on low, small, aquatic plants and animals some of the effects of light than on higher terrestrial organisms, but the comparison of higher and more complex forms with the lower shows that the effects are identical in kind if not in degree. For this reason, and because no one man can know all the parts of the whole subject of physiology equally well, it must still be divided. While the following pages will be devoted mainly to the study of plants, the reader should bear constantly in mind that, at the same time that there are special vital activities—special manifestations of life—according to species and individuals as well as "kingdoms," there are also general vital activities common to all living things. Before passing to any consideration of these in detail, it will be well to enumerate the conditions essential to life, to consider the material and the structure in which life is resident and which manifest it, and to realize that these conditions, this material and structure, are the same for all living things.

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* Sachs, J. von. Lectures on the physiology of plants, English translation, by H. M. Ward, p. 650. Oxford, 1887.

† Verworn, M. Allgemeine Physiologie, two editions. English translation, by Lee. General Physiology, New York, 1899. Davenport, C. B. Experimental Morphology. Parts I. and II., New York, 1897, 1899. Others to follow.

I. THE CONDITIONS ESSENTIAL TO LIFE

These may be comprehended under five headings:—

1. Proper Food—(a) the source of the materials of which the body is built, and
   (b) of the energy by which the body is built and operated.
2. Water—(a) the vehicle of the food-materials and of the foods absorbed into the body and transferred from part to part, and also
   (b) an indispensable component of actively living protoplasm.
3. Proper Temperature—which makes possible the vital, *i.e.* the chemical and physical, changes which must go on within the body, and in all of its parts, lest inaction and death ensue.
4. Proper Illumination—which furnishes the organism with the forms of energy—physical and chemical—thermal, luminous, and actinic—of which it is directly or indirectly in need.
5. Proper Freedom—freedom from mechanical and other disturbances which would interfere with its supply of food, water, warmth, and light, and prevent it from carrying on its natural functions.
   (To this list some might wish to add Oxygen, but this is included under the first heading.)

The many forces and matters included in this brief summary are not merely passively essential to life; they actively stimulate all living organisms. The organisms are sensitive, and respond to these stimuli. Supplying food to animal or plant is applying a stimulus, as well as providing the means to further and continued action. The response to the stimulus may vary with the organism, be immediate or delayed, be external and visible to the eye, or merely internal; but every organism lives, both because the conditions make living possible, and also in accordance with and in response to the many and diverse stimuli exerted upon it by these conditions. The different reactions of different organisms to the same stimulus do not imply any special or peculiar vital force; on the contrary, they imply the special or peculiar structure of these different organisms. The force of gravitation pulls some things down, but it is the same force which keeps other things up. The Eiffel Tower, constructed in opposition to the force of gravitation, stands now because of it. So all living organisms, subjected to like forces and supplied with like materials, behave according to the characteristic habits of each species and the peculiar habits of each individual.

II. THE LIVING MATTER AND THE ACTIVELY LIVING STRUCTURE

As Hertwig has so strongly emphasized,* the living and active protoplasm is to be regarded not as a chemical compound or an association of chemical compounds, but rather as an orderly arrangement of these into a definite structure, of which water is an indispensable constituent. Some of the water contained within the cell should be considered to be as much a constructive constituent of the living protoplast as the water is of the crystal of copper sulphate. As, without a certain amount of water, one can never have crystals, no matter how much copper sulphate may be present, so also, without the necessary amount of water we can never have active protoplasm. When the water of constitution is withdrawn, all the activities of the cell cease with the demolition of its structure. Dehydration is fatal to nearly all plants and their parts, rapid dehydration is fatal to all; but ripe seeds, in which all the vital activities are greatly reduced as the embryo attains the stage of development characteristic of the species, can without injury slowly give up nearly all the water which they contain. By this means the protoplasmic structure, the arrangement of the protoplasmic particles, necessary to active life, is sufficiently altered to cause an entire suspension of all activities. In a climate of average humidity water will still remain in air-dry and wholly dormant seeds, as may be shown by weighing them air-dry and reweighing after they have been dried for an hour in an oven at a temperature of 70° C., or for a longer time at room temperature in a desiccator. The following table, quoted from Schröder,* shows the percentage of water contained in ripe and air-dry grass "seeds," thus—

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* Hertwig, Oscar. Die Zelle und die Gewebe, Bd. I., p. 15. The Cell—translation by Campbell, vol. I.

Hordeum vulgare,	14.65%
Triticum durum,	14.63%
Triticum spelta,	14.40%

This amount, though considerable, is less than the constitutional water of the active protoplasmic structure, and hence all vital activity is extremely slight. With the restoration of the water of constitution, and after the lapse of a part if not all of the usual "resting period" of the seeds, the vital functions will be resumed.

The spores of many of the lower plants are also able to bear the withdrawal of the water of constitution without permanent injury, and like seeds, they can withstand during this period of inaction degrees of heat and cold, amounts of poisonous gases, and other influences which at other times would be fatal to them. The dry seeds of peas and beans, the grains, etc., and the dry spores of various fungi, can be subjected for hours to a temperature of about 100° C. without destroying their germinating power, although about half that temperature would in fifteen minutes be fatal to them after germination. The active cells of the great majority of bacteria will be killed in ten minutes by a temperature of 50 to 60° C., or in five minutes by a temperature of 70° C., although the dry spores of *Bacillus anthracis* succumb only after heating for three hours at 140° C.*

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* Untersuchungen aus dem Botan. Institut zu Tübingen, Bd. II., p. 10, 1886.

During the period of nearly complete dryness seeds and spores are still alive, but the evidences of life are extremely difficult to detect. Respiration goes on very feebly indeed in air-dry seeds, yet that these seeds do respire is claimed by Kolkwitz† as the result of refined methods of collecting and measuring small quantities of carbon-dioxide; but seeds containing still less water respire even less, and with no constitutional water all respiration ceases.

Since water is in itself lifeless, its presence or absence is merely a condition which makes life possible or the reverse. Life may be resident in some other of the chemical compounds composing protoplasm, but it will manifest itself only when water is present in sufficient amount. Although the ability to form crystals of the characteristic size, form, and color resides in molecules of copper sulphate and not in molecules of water, no copper sulphate crystals will form until $CuSO_4$ molecules are accompanied by a sufficient number of water molecules to make the crystalline structure a physical possibility. Another comparison, if not pressed too far, may also assist in emphasizing and elucidating this matter. The living protoplasm deprived of water may be likened to the disconnected parts of a machine; it may be heated or chilled or subjected to other kinds of harsh treatment without greatly, if at all, affecting it; but set up the machine, furnish it with energy, and it will work—give an abundance of water to the protoplasm so that it may set itself up into a machine, allow it to furnish itself with energy, and it will work. But though water is indispensable to the carrying on of the vital functions, it is not in all cases essential to the preservation of life.

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* Fischer. Vorlesungen über Bakterein, Jena, 1897, p. 72. English trans. by Jones, Structure and functions of bacteria. Oxford, 1900, p. 76.

† Kolkwitz, R. Über die Athmung ruhender Samen. Ber. d. D. Bot. Ges., Bd. XIX., 1901.

The vital functions may be suspended, without deterioration of the germinating power of the resting body, for periods varying with the species and in some instances astonishingly long. As a matter of safety, the dry seed or spore should regularly retain its vitality at least for somewhat longer than the usual period during which, by reason of heat, or cold, or drought, active life is impossible. Some seeds may retain their germinating power for much longer times, during which all activities are practically suspended. The majority of authentic cases of suspended activity indicate that beyond thirty years exceedingly few seeds remain alive. It is probable that during these periods of apparently suspended activity, some of the vital processes still go on, so slowly as to be unnoticeable, but resulting ultimately in the consumption or destruction of essential constituents of actively living protoplasm. Seeds which have lain dormant too long have, therefore, lost essential constituents; their actively living protoplasm cannot be reconstructed when water is added; they have lost their power of germination.

The survival of successive periods of drought by certain species of mosses, liverworts, lichens, algæ, and bacteria in their vegetative instead of spore forms is even more remarkable. The spores and seeds which survive periods of inaction have at all times few functions to perform. The vegetative forms of mosses, liverworts, lichens, algæ, and bacteria have to perform, or to prepare for, all the functions of these organisms. It is all the more remarkable, therefore, when they are regularly able to survive, though all their vital functions may be suspended. This implies a considerably greater power of endurance than is possessed by the vegetative parts of more highly organized plants. Yet in California, and in other parts of the world, where there are several months in each year when no rain falls, though in other months it falls abundantly, plants growing in uncultivated places must be able to adjust themselves to the periods of enforced inaction. So far as our Pacific Coast plants are concerned, this is, however, an uninvestigated subject, one which offers many attractions to the physiologist.*

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* In the year book of the U. S. Dept. of Agriculture, 1897, Whitney reports (p. 129) a comparison of the soils and subsoils of the eastern and western States. From this he draws the conclusion that the absence of a heavy subsoil, and the spontaneous formation of a "mulch" of dust on the surface, cause the plants of arid regions, and those living where there is a long dry season, to secure for their needs a much larger percentage of the total annual rainfall than is available for eastern plants. In the East, the heavy subsoil drains off about half of the total rainfall, and the remainder is still further reduced by evaporation. But though all this is undoubtedly true, yet the perennial plants themselves must also show adaptations to the climatic conditions of the far West and of California, and these deserve study by physiologists.

CHAPTER II

RESPIRATION

ENERGY is necessary to the operation of every machine, whether it be an engine or a living organism. The engine is supplied with energy directly or indirectly through the intelligent action of a living organism; the living organism supplies itself with energy. In both cases the energy is ordinarily supplied by the same means, mainly by combustion or oxidation, and the energy thus liberated is applied either directly or indirectly in the same form. In the case of the steam-engine the energy or power is applied indirectly, the heat resulting from the combustion of fuel being utilized in the conversion of inelastic water into perfectly elastic, compressed, and hence active, steam. In the living organism the energy resulting from combustion is applied directly in the various kinds of work done by the living organism either within or outside of its own body.

Energy must be supplied to the engine for two purposes: first, to overcome the resistance (friction, inertia, etc.) of its own parts; and second, to enable it to overcome the resistance offered by the materials upon and in which it works. For two purposes also energy must be supplied by the living organism for its own use: first, to continue living; and second, to enable it to overcome the resistance offered by the materials upon and in which it works. Let us think first of the need of energy to continue living. Living consists in maintaining the equilibrium between constructive and destructive influences. This implies *work,* in the physicist's sense. So long as the constructive influences overbalance the destructive the organism gains in some way—grows, or increases in weight, or moves, or reproduces. To gain thus, to do any of these things, the organism needs energy. When the destructive influences overbalance the constructive the organism loses in some way—it ceases to grow, or decreases in weight, or moves less, or fails to reproduce. The destructive influences result in the liberation of energy, the constructive in the storing of energy. The liberation of energy implies previous construction, for the generation of energy from nothing is inconceivable. The chief source of energy in the organism is combustion, the destruction by oxidation of not merely already existing, but really of previously formed substances. The direct result of oxidation is the evolution of heat.

To the oxidation which goes on within the living organism is given the name RESPIRATION. The interchange of gases between the blood of higher animals and the air, which takes place at the lungs or gills, is but a part of the process of respiration. The oxygen taken up by the blood at these surfaces exposed to the air is transferred by the circulation of the blood to the tissues and cells by which it is used. The oxygen is used by combining it with other substances, by oxidizing these substances. Respiration is physiological oxidation, or combustion, as distinguished from such oxidations as take place under ordinary conditions spontaneously. The element sodium, when exposed to the air, will unite with the oxygen without heat, light, or any other known form of energy being applied to encourage the union. Animal and vegetable substances will not so unite, the oxidation must be encouraged, and it will take place outside the living body only at a temperature considerably higher than that developed within the body of any living organism. In respiration we have, then, a process which differs from ordinary oxidation in the conditions under which it takes place. The results, however, are the same. In respiration we have to do not only with the affinity of oxygen for certain elements and compounds, but with the need of the living organism for energy. The organism must be actively living in order that the oxygen of the air may be made to unite with those substances in the body from which energy is to be liberated. Respiration may be artificially continued, with the liberation of energy, only for a short time after the death of the organism as a whole, only until the death of the cells composing the body. The cells need free oxygen during life; they remove it by combining it with complex combustible compounds. So long as the removal of free oxygen by combining it with other substances takes place, so long will oxygen continue, in obedience to the laws governing the diffusion of gases, to enter the cells. The combination of oxygen with combustible substances at temperatures below those at which these substances would spontaneously oxidize, takes place in living cells and is accomplished only by them.

Though the living cell is supplied with oxygen by purely physical means, by diffusion, the continued supply of new molecules of oxygen is contingent upon its continued consumption by the cell. The supply must make good the lack produced by oxidation, the rate of oxidation must equal the demand for energy, and the amount of work done in the cell will always be directly proportioned to the amount of energy it can liberate. The initiative, however, will always come from the living cell, because oxidation by respiration is not dependent solely upon the mutual affinities of oxygen and the substances to be oxidized. The activity of the cell controls the activity of respiration (not *vice versa*), and the supply of oxygen, normally exactly equal to the consumption, is also controlled by the cell. An excessive supply of oxygen, which for experimental purposes may be artificially furnished, will affect the respiratory only as it, at the same time affects the other activities of the cell. Each kind of cell and each kind of organism will have its own optimum, maximum, and minimum, any departures from which will characteristically affect the cell and the organism. The percentage of oxygen in atmospheric air (about 20%) is approximately the optimum for the majority of land organisms, though for a small number this amount, and even much less than this, is fatal. The amount of available free oxygen necessarily varies with the habitat, plants living on mountain-tops, and in water, having less than those living on the land at ordinary elevations. But the successful existence of plants at different elevations and depths shows that they are capable of supplying themselves with what they need.

Within the limits in which normal respiration is possible, plants, and hence their component cells, will supply themselves with adequate amounts of oxygen, an excessive proportion suddenly supplied causing, in some plants, merely a greater accumulation of oxygen, unaccompanied by greater respiration,* in the cells; in others, more rapid respiration as indicated by higher temperature, etc. On the other hand, sudden reduction of the amount of oxygen may cause a diminution of the respiratory activity.

So long as the general conditions for life continue in adequate degree, there is no cessation of respiration in plants or in animals. This is true of the resting forms—buds, bulbs, tubers—although in them the rate of respiration is much lower than in active forms. It is possible to force these resting forms by various means into activity, but it is not possible, after they mature, to continue the rate of respiration which they possessed during their development. The forming bud, bulb, or tuber is composed of cells actively working, needing much energy with which to work, and respiring rapidly in order to secure this. With the approach of maturity of the parts, the work to be done, the need of energy, and the rate of respiration, diminish, no matter how favorable to continued activity the external conditions may be. This decrease in respiration, and in the other functions, is largely due to the influences of its environment upon all the functions of the organism as a whole. The organism prepares itself for the regularly recurring periods of drought, heat, or cold; one activity after another is suspended accordingly. After a period of rest, it is possible to force these forms into activity even after the lapse of much less than the usual time. Lilac branches, cut from the bushes late in autumn, can be forced by Christmas time to develop the flowers and leaves already formed. This forcing is accomplished by placing the ends of the cut branches in jars of water and keeping them in a warm, damp, not too brightly lighted place. This experiment, familiar enough to the florist, results in the resumption of active respiration after a period of tardy respiration shorter than usual; it does not continue the respiratory and other activities at the rate prevailing during the formation of the parts.

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* Pfeffer's Handbuch der Pflanzenphysiologie, 2te Auflage, Bd. I., p. 547, 1897. Eng. transl. by Ewart, vol. I., p. 539, 1900.

Respiration is a process conducted and regulated by the living protoplasm of the cells. It will not go on indefinitely and independently however favorable the physical conditions may be. It can be artificially increased only by stimulating the protoplasm to greater activity; it will be increased whenever the protoplasm becomes more active. The respiration of plants and plant-cells can be artificially reduced only by reducing the general activity of the living protoplasm. This may be accomplished by the same means as the animal physiologist employs—by applying a local or general anæsthetic, by lowering the temperature, by preventing movement, etc. In most plants and plant parts the forced cessation of normal respiration immediately precedes, and is itself the cause of, death. In certain plants—for example, germinating peas—intramolecular respiration* may temporarily take its place; in certain others—for example, anaerobic bacteria†—intramolecular respiration is the normal mode.

Normal respiration cannot, however, be entirely suspended in plants or plant parts without profound changes taking place which sooner or later will result in death. The reduction of normal respiration to an extremely low rate, if not its entire suspension, unaccompanied by any other means of obtaining energy, regularly takes place in the ripe seed, but only when the cells composing the seed lose the water which is an essential constructive constituent of living protoplasm.

In warm-blooded animals the object of respiration is twofold—the maintenance of a certain (normal) body-temperature and the production of energy for doing work. In cold-blooded animals and in plants the object of respiration is solely the latter. The average body-temperature of plants is in general nearly the mean daily temperature of their environment, and it will vary within certain limits accordingly. The variation in the body-temperature of plants will

* See page 27.

† See page 26.

be large or small according to the environment. Submerged aquatics will vary least, floating aquatics more, and terrestrial plants most; but as the temperature of small, still bodies of water (pools, etc.) varies considerably, so the body-temperature of the organisms living therein will vary, warmed by the sun and cooled during the night. The body-temperature of the larger terrestrial plants is likely to be higher at night (except in the exposed surfaces) and lower in the day, than that of the surrounding air. Owing to the very great external surface of the larger plants in proportion to their mass, radiation from them is rapid, and a body-temperature independent of their environment could be maintained only at great expense of material laboriously collected and elaborated. Plants work economically, must do so, and such extravagance is avoided.

Heat is the form in which the energy set free by respiration usually makes itself evident, but it does not necessarily follow that only so much energy is liberated as is recognizable as heat, or that this is the only form in which energy is liberated. Only that energy becomes evident as such which is not at once used. To determine the amount of energy liberated in respiration, it is necessary to know and to measure the material products of respiration.

The substances ordinarily engaged in the process of physiological oxidation are the highly complex nitrogenous and non-nitrogenous compounds elaborated by the organism. The ordinary products are carbon-dioxide, water, and various small amounts of several other substances, *e. g.* oxalic acid. Since the production of energy rather than of any particular compounds is what is striven for in respiration, and since the substances acted upon by free oxygen are different in different plants and cells, the products will differ accordingly.

Although the oxidation of nitrogenous matters also takes place, it is mainly the non-nitrogenous contents of the living cell which are involved in physiological oxidation. In the animal body, the oxidation of organic nitrogenous compounds (proteids) results in the production of urea and of other similar substances no longer usable and presently cast off from the body. In plants, the elimination of these products is more economically accomplished, for they furnish the foundations for the re-synthesis of albuminous compounds, as will be discussed under the subject of nutrition (see page 71). These waste substances are removed by transforming them synthetically into useful compounds.

The non-nitrogenous substances which become oxidized are the fats and oils, the starches and sugars. The oxidation may first convert the hydrocarbons into carbo-hydrates, with the liberation of energy and the formation of by-products, carbo-hydrates and by-products then becoming still further oxidized with the liberation of still more energy. While respiration is going on, the other functions in operation also may involve the use, by chemical change, of some of each substance produced in respiration and the formation in the cell of other substances not the products of respiration at all. It is therefore evident that to ascertain the material products of respiration is hardly less difficult than to determine the amount of energy liberated. To isolate any physiological process for purposes of study is impossible, for each process is normal only when accompanied by all the processes normally going on at the same time. The products of one set of chemical activities in the living body may enter wholly or partially, simultaneously or successively, into other chemical activities. The end products can be recognized and measured with comparative ease, but to tell exactly where or how they are formed is much more difficult and not now entirely possible.

Water and carbon-dioxide gas are the chief products of the physiological as also of other forms of combustion of carbon-containing bodies. They are formed whenever a sufficient amount of oxygen is united with the higher carbon compounds. In organisms living under such conditions that the air can penetrate to all their parts, enough oxygen will always be present for such complete decomposition. Under ordinary conditions oxygen does not unite of itself with the combustible compound, and if active (nascent) oxygen is present at all in the cell it is only in amounts insufficient to accomplish the whole result.* The union of oxygen and the substances to be oxidized is accomplished by the living cell. How this is done is not known, though conjectures are not lacking. Whether the combustible substances and the oxygen are divided into such small particles and so intimately associated in the living protoplasm that union takes place spontaneously, or whether the oxidation is accomplished by enzyms, or whether more readily or spontaneously oxidizable substances are first formed from sugar (perhaps by the action of an enzym), is not known, though there is a certain amount of evidence in favor of each hypothesis. All that is known is that sugar, or some similar substance, and oxygen, unite, forming as end-products mainly carbon-dioxide and water. The following reaction, without indicating what intermediate stages there may be, if there are any, shows the material results:

$$C_6H_{12}O_6 + 6\ O_2\ (+Aq) = 6\ CO_2 + 6\ H_2O\ \ (+Aq)$$

(Aq. represents the water in which the sugar is dissolved in the cell: it does not enter the reaction. The 6 H_2O may unite with this or these molecules may pass off as vapor, as in ordinary combustion, being kept in a state of vapor by the heat liberated.)

Since other substances than sugar are also oxidized physiologically in the cell, there are also other products of sorts and in quantities varying with these. The commoner of these minor products are oxalic, malic, and citric acids, which accumulate in considerable quantities in certain plants (*e. g.* in the leaves of *Oxalis acetocella* and in the *Crassulaceæ*, in apples, etc., and in the citrous fruits—lemons, limes, oranges, etc.), or are converted into salts (*e. g.* calcic oxalate, crystallizing out of the solutions in which it is formed in the cell), or undergo other changes (*e. g.* further oxidation).

In all organisms the oxidation of nitrogenous as well as non-nitrogenous compounds occurs in normal respiration. The proportional amounts of these two groups of compounds physiologically oxidized varies with different organisms. In the majority only organic and highly complex compounds are made to yield the needed energy, but in some organisms much simpler inorganic compounds suffice, and in a few now known (more may later be discovered) the carbon-containing compounds are not used at all.

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* **Pfeffer, W. Oxydationsvorgänge. Physiol. of Plants, Vol. I., pp. 54-56.**

The nitro-bacteria, as shown first by Winogradsky,* oxidize simpler nitrogen compounds in order to liberate the energy which they need, employing carbon-compounds only in the synthesis of food to be used in the construction of their living bodies. One set of nitro-bacteria oxidize ammonia, or compounds of ammonia, to nitrous acid, the first and last steps of the process being indicated by the reaction—

$$2\ NH_4OH + 3\ O_2 = 2\ HNO_2 + 4\ H_2O$$

Another set oxidize the nitrous acid, or its salts, to nitric acid thus—

$$2\ HNO_2 + O_2 = 2\ HNO_3$$

The sulphur-bacteria (*Beggiatoa*, etc.) obtain most if not all of their kinetic energy by oxidizing sulphur compounds. Thus they precipitate sulphur in their own bodies by oxidizing the sulphuretted hydrogen (H_2S) present in the waters in which they live.† If the supply of the gas remain sufficient, the sulphur will accumulate as a reserve supply in the cells; if it decrease, the reserve sulphur will be oxidized and, uniting with water, will form sulphuric acid, or its salts, thus—

$$\begin{aligned} S + O_2\ (+ Aq) &= SO_2\ (+ Aq) \\ 2\ SO_2 + O_2\ (+ Aq) &= 2\ SO_3\ (+ Aq) \\ SO_3 + H_2O\ (+ Aq) &= H_2SO_4\ (+ Aq) \end{aligned}$$

Those bacteria (*e.g.* *Crenothrix*) which, living in water rich in iron, deposit iron in some form in or upon their own bodies, may obtain their kinetic energy by physiologically oxidizing ferrous compounds, presumably ferrous oxide to ferric oxide.*

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* Winogradsky, S. Recherches sur les organismes de la nitrification. Annales de l'Inst. Pasteur, IV., V., 1889-91—and other papers.

† Winogradsky, S. Über Schwefelbakterien. Botanische Zeitung, 1887. Beiträge zur Morphologie u. Physiologie der Bakterien. Leipzig, 1888.

Other bacteria may be discovered which, needing carbon and nitrogen compounds only to supply the constructive elements of protoplasm, obtain energy by oxidizing other substances present in solution in the waters in which they live, and therefrom absorbed into their own bodies.

The essential product of respiration, the one which distinguishes it from all the other functions of the living organism, is kinetic energy. The material products vary in kind and in quantity according to the nature of the organism and the substances which can be affected. Ordinarily these substances are complex compounds elaborated within the body of the respiring plant. That this is not essential is shown by the successful existence of bacteria which oxidize nitrogen, sulphur, iron, and possibly compounds of other elements. These, though necessarily absorbed before they can be acted upon, are not first elaborated by the cell.

Free oxygen is not necessary to all organisms or to all cells. The hæmoglobin of the blood is a complex compound from which some of the oxygen, only loosely held, can be readily given off where oxidation for the supply of energy is needed. Similarly the color products of certain bacteria (*e. g.*, *Bacillus brunneus*) are reserves of oxygen which become used when there is no longer an adequate supply of free oxygen.† From colorless compounds also, the cells at depths in the tissues of animals (perhaps also of plants‡), to which free oxygen penetrates only in insufficient amounts if at all, obtain by decomposition the energy needed. These decompositions are not necessarily effected to secure oxygen for oxidation of other substances, but the decompositions themselves release as kinetic the potential energy which was needed to hold the complex substances together.

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* Winogradsky, S. Über Eisenbakterien. Bot. Zeitung, 1888. Molisch, H. Die Pflanze in ihren Beziehungen zum Eisen, Jena, 1892. See also Miyoski, M. Studien über die Schwefelrasenbildung und die Schwefelbacterien der Thermen von Yumoto bei Nikko and Über das massenhafte Vorkommen von Eisenbacterien in den Thermen von Ikao. Journal Coll. Science, Imp. Univ., Tokyo, vol. X., pt. II., 1897.

† Ewart, A. J. On the evolution of oxygen from colored bacteria. Journal of the Linnean Society, XXXIII., p. 123, 1897.

‡ Pfeffer, W. Berichte der Math-phys. Classe der Königl. Sachs. Gesells. der Wissensch. zu Leipzig, 27 Juli, 1896, p. 383.

The mutual attraction of one atom of carbon and two of oxygen is so great that the molecule of carbon-dioxide is very stable as well as very simple, for the "affinities" of the carbon and oxygen are "satisfied." In such complex compounds of carbon, hydrogen, and oxygen as the starches, sugars, etc., the affinities of the component elements are not satisfied; the compounds are much less stable, as is shown by their ability to take up more oxygen. At ordinary temperatures, however, and under ordinary conditions, these compounds are stable. They owe their stability to the mutual affinities of their component atoms, which exert an attraction upon one another sufficiently powerful to hold them together in definite form. When the atoms are separated from one another and arrange themselves closer together in simpler forms in space, their "bonds" or "affinities" are more completely "satisfied," they unite more perfectly, oxidation takes place in the rearrangement, and energy is accordingly liberated and made available for other purposes. Energy is "stored" in the starch, or sugar, or oil molecule; the kinetic energy (solar or other) employed in the construction of the molecule remains in it as potential energy, holding the atoms together. The destruction of the molecule results in the liberation of so much kinetic energy as was employed in constructing it from the simple compounds worked upon.

The complete oxidation or combustion of a gram of dextrose (sugar), resulting in the formation of carbon-dioxide and water as represented in the following reaction—

$$C_6H_{12}O_6 + 6\,O_2 = 6\,CO_2 + 6\,H_2O$$

liberates 3,939 small or ordinary calories, or mechanical units of energy in the form of heat.* (A calorie (c) is the heat required to raise 1 gram of water 1° C. in temperature, a great calorie (C) is the heat required to raise 1,000 gr. (1 Kilo) of water 1° C.*). But since a gram of dextrose may contain a very different number of molecules from a gram of any other substance, and since the liberation of energy is due to the oxidation of molecules rather than of mere weights of a substance, it is well to convert these figures into a form which will enable one to compare the yield in energy when the substances are similar in quantities. Thus, by using the molecular weights of the compounds to indicate the number of grams, we have a common basis for the comparison of the heats liberated, namely, the gram-molecule. Thus the molecular weight of dextrose is 180, obtained thus—

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* Rechenberg, C. von. Über die Verbrennungswärme organischer Verbindungen. Inaug. Diss., Leipzig, 1880. See also Pembry, M. on Animal Heat in Schafer's Text-book of Physiology, vol. I., Edinburg, London, New York, 1898. Here the literature is fully given.

atomic weight of C = 12 $C_6 = 72$
"   "   " H = 1 $H_{12} = 12$
"   "   " O = 16 $O_6 = 96$

180 = molecular weight of dextrose ($C_6 H_{12} O_6$)

3,939 calories × 180 = 709,020 calories = 709.02 Calories. The heat of combustion (complete oxidation) of 1 gram-molecule, *i. e.* of 180 grams of dextrose, is then 709.00 Great Calories (C.)

This reaction and the production of this amount of heat take place only in the presence of sufficient quantities of free oxygen. Molecules more complex than those of carbon-dioxide and water, though simpler than sugar, may be formed from sugar without free oxygen or with free oxygen in smaller proportions than 6:1. Complete oxidation (normal respiration) yields the largest amount of energy, less profound changes yield less energy. Thus the decomposition of sugar by yeasts, according to the following reaction,

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* It may be interesting to compare the amounts of heat liberated by burning 1 gram of different substances, thus:

1 gram	bread crumbs (contain some proteid)	3984	calories.
1 "	butter	7264	"
1 "	wood-charcoal (mainly carbon)	8080	"
1 "	hydrogen	33881	"

which represents only in simplest terms the nature of the chemical changes—

$$C_6H_{12}O_6 = 2\,C_2H_6O + 2\,CO_2$$

(alcohol)

forming without oxygen two molecules of alcohol and two of carbon-dioxide from one molecule of dextrose—yields only 67 calories per gram-molecule.*

The decomposition of one molecule of dextrose into one molecule of butyric acid, two of carbon-dioxide, two of hydrogen, which is accomplished by a considerable number of bacteria and may be represented by the following reaction—

$$C_6H_{12}O_6 = C_4H_8O_2 + 2\,CO_2 + 2\,H_2$$

(butyric acid)

yields about 75 calories per gram-molecule.†

Bacteria forming acetic acid, acting on dilute solutions of ethyl alcohol in the presence of free oxygen, partially oxidize the alcohol and decompose it into acetic acid and water, thus—

$$C_2H_6O + O_2 = C_2H_4O_2 + H_2O$$

liberating 125 calories‡; but if the alcohol were completely oxidized, as in ordinary combustion, the reaction would be

$$C_2H_6O + 3\,O_2 = 2\,CO_2 + 3\,H_2O$$

and the heat liberated would be nearly three times as much, about 325 calories per gram-molecule.

In these figures we have indices of the relative values of complete and incomplete oxidations, and of oxidations and decompositions, as sources of energy in the form of heat. These figures are indices, to be trusted only so far as relative, not exactly proportional, values are concerned; for the chemist can control all the conditions under which he makes a combustion in his laboratory and determines the number of heat-units liberated; he can so regulate the process that there shall be no by-products and that no other compounds are included in the reaction than those upon which he has determined to experiment. In the plant, on the contrary, other substances than dextrose may become oxidized, or the oxidation of dextrose may be incomplete. In the laboratory one can deal with definite quantities of isolated substances; in the living organism indefinitely known quantities of many substances together are acted upon. Animal physiologists have done much more in this direction than have plant physiologists, and the high organisms which they study are better suited for the purpose than are plants. The relatively high body-temperatures of warm-blooded animals permit direct temperature determinations from weighed quantities of known foods eaten, as well as calculations from the amounts of oxygen needed to effect combustions or decompositions. Thus the animal physiologist can check the results obtained by one method with those obtained by other methods. The results of animal physiologists indicate that only about 95% of the calculated yield of energy from oxidation* appears as heat. So then we must regard these figures as somewhat too high, but their suggestive value is great whatever must be admitted as to their exact numerical value.

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* Rechenberg, l. c., p. 66.

† *Ibid.*, p. 67.

‡ Quoted from Berthelot in Biedermann's Chemiker-Kalender for 1897, p. 193 of the Beiträge.

The larger organisms demand for the normal execution of their functions more energy than can be supplied by the rearrangement of the component atoms of already furnished molecules; they must oxidize these molecules, and the more complete the oxidation, the greater the amount of energy liberated. Some of the smaller organisms supply themselves with adequate amounts of energy by the destruction of complex compounds within their own living cells. Probably some of the cells of all organisms have recourse, at times at least, to the same means of securing needed energy, and when free oxygen is not obtainable the majority of organisms can continue living for a time by so doing. From this the general inference may safely be drawn, that the ability to obtain needed energy by the destruction of complex substances in the cells is inherent in all organisms; that in the majority of organisms and of their component cells this power is little needed and hence is practically undeveloped; but that, owing to the position of some cells deep in the tissues of many of the larger organisms, and to the peculiar habits of some of the lowest organisms, these are obliged to obtain needed energy in this way and have developed their inherent powers to a high degree.

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* See Pembry in Schäfer's Physiology, vol. I., pp. 836-7.

Intramolecular respiration is the name given to this mode of respiration, a term not entirely satisfactory, for it is not explicitly descriptive. The German term *Spaltungsathmung* is in this regard much more satisfactory, but it is not concisely translatable. Ordinary respiration, physiological oxidation or physiological combustion, is aerobic respiration—respiration which is dependent upon free oxygen, and which yields the needed kinetic energy only by the union of free oxygen with combustible substances. Intramolecular respiration, physiological simplification of complex substances, physiological rearrangement of atoms, is anaerobic respiration—respiration which takes place only when free oxygen is present in insufficient quantities or is altogether absent. The results of the two processes are the same in kind—the liberation of the kinetic energy necessary to continue living—but not the same in degree, as the figures above quoted show.

It is now about one hundred years since intramolecular respiration was first observed,[*] but only within the last few years has the connection between the two means of securing energy been demonstrated. In addition to the animal and plant physiologists, our present knowledge is due also to Pasteur and other bacteriologists, for they have shown the peculiar habit of a large number of micro-organisms in actively living only where free oxygen is absent. We have a chain of allied processes: *first,* physiological oxidation, or what may be called **inter**-molecular respiration, the normal respiration of most organisms; *second,* physiological rearrangement of atoms into simpler molecules, **intra**-molecular respiration, the mode of respiration which many cells and a good many organisms have recourse to under stress of circumstances; *third,* physiological rearrangement of atoms into simpler molecules, also really intramolecular respiration, the anaerobic normal respiration of a comparatively small number of invariably low organisms.

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[*] Rollo. Annales de Chimie, t. 25, 1798.

INTRAMOLECULAR RESPIRATION

Having examined the first of these allied processes as thoroughly as our limits allow, let us pass to the second. From experiments hitherto conducted, it would seem that the germinating seeds of higher plants are better able to survive without a copious supply of oxygen than are the other parts. This is what might be expected, for the embryo in the seed, when it becomes active in germination, is a very vigorous organism, usually well supplied with just such foods as may be readily broken down into simpler compounds. The seeds of pea, for example, stimulated to germinate by being soaked in water at room-temperature for twelve or fifteen hours, will continue to respire actively for forty-eight hours or longer, even in a vacuum, producing carbon-dioxide in nearly the same quantity as under the same conditions of temperature, etc., in ordinary air. Of course some air containing free oxygen will be carried into the vacuum by the peas, but this will very soon be entirely consumed in normal respiration, and the continued supply of energy must be obtained by intramolecular respiration.* Comparative investigations have shown that different plants and different organs vary considerably in their ability under stress to substitute intramolecular for normal respiration, and that in very few of the higher plants is intramolecular respiration, as measured by the yield in carbon-dioxide, so effective as normal respiration.

For all of the higher plants prolonged intramolecular respiration is impossible. To what this is due is not wholly clear. The substances first broken up in intramolecular respiration are the same as in normal respiration, namely, the sugars, starches (after conversion into sugars), and the fats and oils; but later the proteid substances enclosed in the cell, and finally the living substance itself, are decomposed to supply needed energy. Whether the cessation of intramolecular respiration in experiments upon higher plants, and the consequent death of the organism, are due to the destruction of a part of the living substance, or whether they are due to the production in the cells of poisonous substances, cannot now be positively asserted. Certain it is that for higher organisms intramolecular respiration is a function very limited in importance, taking place only under the stress of continued need of energy, in the absence of an adequate supply of free oxygen, and capable of being maintained for comparatively brief periods only. Like normal respiration, it is carried on solely by the living protoplasm, more or less actively according to the greater or lesser activity of the protoplasm; the substances decomposed are like those oxidized in normal respiration and differ in different species of plants; the products differ according to the plant, the conditions under which it acts, and the substances acted upon.

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* For directions for laboratory and demonstration experiments on this subject consult Darwin & Acton's Practical Physiology of Plants; Moor's translation, under similar title, of Detmer's Pflanzenphysiologisches Praktikum, or the special papers on the subject cited in Pfeffer's Handbuch der Pflanzenphysiologie, and its English translation, and also in Ganong's and MacDougal's manuals.

Besides carbon-dioxide, alcohol may be produced in considerable amount—suggesting the connection between fermentation and intramolecular respiration—and also organic acids, together with small amounts of many other compounds. In germinating peas, the alcohol produced may equal as much as 5% the weight of the moist seeds,* enough to give some support to the hypothesis suggested above that it may be the accumulation of the poisonous products of intramolecular respiration which, as we shall see is the case in fermentation (pp. 30-37), brings about the cessation of respiration and the death of the organism.

Between those plants for which aerobic respiration is indispensable to normally active life, and for which anaerobic respiration is only a means of maintaining life over unfavorable periods, and those for which anaerobic respiration is similarly and equally indispensable, there are all connecting stages. These are found among the lower plants, especially among the fungi; but, as before stated, in all large multicellular organisms, especially among animals, there are probably cells, lying deep in the tissues, which are forced by the positions they occupy to supply themselves with needed kinetic energy by the same means as the anaerobic organisms, namely, by decomposing the complex compounds which they contain. There are, then, cells as well as organisms which are obligate aerobic, facultative aerobic, and obligate anaerobic. The obligate anaerobic cells and organisms live where the access of free oxygen is impossible or difficult: for instance, deep in living tissues, either as component parts of these tissues, or as parasites and saprophytes therein; in the deeper layers of compact soils, in the mud of swamps and marshes, and in the ooze below bodies of comparatively still water, fresh and salt; indeed, wherever there are proper food, proper temperature, and proper freedom.

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* Godlewski. In the Anzeiger der Krakauer Akademie, Juli, 1897. Reviewed in Botanische Zeitung, Sept. 16, 1897.

As in aerobic so also in anaerobic respiration, other processes take place simultaneously with it. These, if not directly caused by respiration, are at all events maintained by the energy liberated in it, and are so closely connected with it that to distinguish between the chemical products of respiration and those of the processes accompanying it, is a matter exceedingly difficult and not yet fully accomplished. Fermentation, decay, and disease at least accompany, if they are not actually a part of, the respiratory processes of certain low plants. Anaerobic respiration, as well as aerobic, is a function of the living protoplasm, which acts upon substances enclosed within its own body, producing simpler substances, of which some remain in the respiring cell while others diffuse out of it. Some of the latter are entirely inactive chemically, like carbon-dioxide and alcohol; others may act upon the substances outside of the cell. In the higher animals and plants the enzyms (like pepsin, diastase, etc.) are produced in connection with the process of nutrition, converting the substances upon which they act into available food compounds; but it is also certain that, among the enzyms produced, there are some which bring about such changes in the surrounding substances that these become available as sources of kinetic energy. For example, the diastase formed in the germinating seed, which dissolves the starch deposited as a reserve food in the seed, converting it into sugar, makes the reserve food available for at least three purposes; *first*, for the construction of nitrogenous compounds (amides and proteids); *second*, for the formation of cell-wall (cellulose); and *third*, for the liberation of energy by aerobic respiration. The production and action of this enzym furnishes material for respiration as well as for nutrition. The enzyms formed by the lower plants are also useful in more than one way, and in many cases one of these uses is undoubtedly the conversion of irrespirable into respirable substances.

FERMENTATIONS

In the group of processes which are commonly called fermentations (alcoholic, lactic, butyric, etc.), the physiologist must study both respiration and nutrition. A thorough understanding of the physiology of fermentation* is impossible without previous thorough knowledge of the chemistry of fermentation. As this chemical knowledge is still incomplete, it is possible to form only general ideas concerning fermentation and the allied processes of decay and disease. The distinction usually made between fermentation and decay is this, that in fermentation there is evolution of gas, whereas, in decay, there is little or none—an artificial and even misleading distinction. Even the attempted distinction between disease on the one hand, and fermentation and decay on the other, is anything but fundamental; for disease, so far as it is the result of the activity of foreign organisms, is nothing more than decay or fermentation carried on by those foreign organisms upon or in the living body of the host.

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* On the subject of fermentation the student may well consult J. Reynolds Green's "The Soluble Ferments and Fermentation." Cambridge, England, 1901. In this book there is a very useful bibliography.

Although at present unable to determine the respective parts taken by respiration and nutrition in fermentation, decay, and disease, let us briefly consider some examples. The fermentation most studied because the most useful is alcoholic fermentation, by which is understood the production of the ethyl alcohol of commerce. The organisms which produce most alcohol from a given quantity of sugar are certain species of yeast (*Saccharomyces cerevisiæ, S. ellipsoideus*), but certain species of *Mucor** (*M. erectus, M. racemosus,* even *M. mucedo*) and bacteria also form ethyl alcohol in considerable quantities. We have already seen that in the forced anaerobic respiration of higher plants (fruits and germinating seeds) alcohol is one of the products. It may therefore be inferred that, like anaerobic respiration, the production of alcohol in fermentation is not peculiar to the plants most used for the purpose, but that the power to produce it is possessed by most, if not all, plants. In the majority, however, this power is undeveloped.

Not only the amount of alcohol but also the nature and the amounts of the other substances produced, determine the availability of a plant for the commercial production of ethyl alcohol. The best yeasts, cultivated under the most favorable conditions, convert about 6% of the sugar used into other compounds than alcohol, *e. g.* glycerine, succinic acid, higher alcohols, ethereal compounds (to which the "bouquet" of wines is chiefly due), etc. Under less favorable conditions, with poorer yeasts, and especially with mixtures of yeasts and bacteria, the amounts and kinds of undesirable by-products increase. The amount of alcohol produced by the bacteria commonly associated with beer, bread, wine, and other yeasts used in the arts in this country, is slight in comparison with their other products; and it is quite as much the kinds and amounts of these other products, as the quality of the fermentable mixture into which they are introduced, which give the peculiar color, texture, flavor, and odor of the different brands. Unless the mixture to be fermented is first sterilized and then inoculated with pure yeast exclusively, every bottle of wine, beer, or other liquor, and every loaf of bread, represents the combined action of yeasts and bacteria. It contains the products, alcoholic and other, so far as they are not driven off or decomposed in the process of manufacture, of all the organisms in the fermenting substance. Preliminary sterilization, the inoculation with pure cultures of yeasts, and fermenting under uniform conditions, are the secret of the uniformly good quality of the well-known German beers and wines. In America such precautions are unusual.

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* See E. Chr. Hansen. Meddelelsor fra Carlsberg Laboratoriet, Bd. I., etc. Untersuchungen a. d. Praxis der Gährungsindustrie. Jorgensen. Die mikroorganismen der Gährungsindustrie, 3te Aufl., Berlin, 1892. E. Gotschlich. Gährungserregung; in Flügge's Mikroorganismen, 3te Aufl., Leipzig, 1896, Bd. I., pp. 219-270. Lafar. Technical Mycology, transl. by Salter. London and Philadelphia, 1898.

The substances acted upon bear a very definite relation to the active organisms. Not all substances are fermentable, not even all substances of the same proportional composition. Though there may be in one substance the same, and the same number of, atoms, these may be so differently arranged that the fermenting organism can act upon the one but cannot upon the other. The yeasts are able to ferment only a limited number of sugars, which are in the main characteristic of the different species.* Some of the yeasts secrete enzyms† which convert starch and cellulose into sugar. Thus ordinary bread yeast, unable to ferment the starch with which it may be brought into contact, secretes an enzym which converts the starch into sugar. Furthermore, cane-sugar cannot be directly fermented, and when present in dough, etc., it must first be acted upon by an enzym, "inverted." The resulting sugar, differing only in the arrangement, not in the number or kind, of atoms, is directly fermentable. These chemical changes can be suggested, though, on account of the by-products already alluded to, not accurately represented, by the following reactions:

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* For tables of these see Flügge's Mikroorganismen, 3te Auflage, Bd. I., p. 204, and the papers by Emil Fischer and collaborators in Ber. d. Deutsch. Chem. Gesellschaft for the last few years.

† Effront, J. Enzyms and their applications. English translation by Prescott, S. C. 1902.

$$\underset{\text{(Starch)}}{C_6 H_{10} O_5} + \underset{\text{(Diastase?)}}{\text{Enzym}} + \text{Aq} = \underset{\text{(Dextrose, etc.)}}{C_6 H_{12} O_6}$$

$$C_6 H_{12} O_6 + \text{Yeast} + \text{Aq} = 2\ CO_2 + 2\ C_2 H_6 O$$

By what has already been said we are led to infer that organisms capable of such decompositions as the above supply themselves by this means with kinetic energy, and can flourish although little or no energy may come from other sources. In fact, the yeasts are facultative anaerobic organisms, demanding free oxygen only when inadequately supplied with the appropriate sugar. The actual fermentation is often only one of a series of processes, first made possible by the inverting action of an enzym upon some not directly fermentable sugar, and followed by other processes for which the fermentation supplies the necessary energy. Buchner and his collaborators* have demonstrated within the last few years that the alcoholic fermentation by yeast is accomplished by an enzym (zymase) which splits the sugar into carbon-dioxide and alcohol, releasing energy which the yeast cells use. This discovery furnishes the ground for the hypothesis that all respiration, not merely alcoholic fermentation, is carried on by the living cell through the agency of enzyms (see p. 19).

The yeasts are more profitable for the commercial production of alcohol, not only because of the larger amount of alcohol which they will produce from a given quantity of sugar, but also because they can continue their rate of production in the presence of a larger amount of alcohol than most organisms can survive. The species of Mucor studied by Hansen† produce only from 3% to 8% of alcohol, whereas the most active species of yeast can produce 14%, although their activity decreases with 12%. It is obviously impossible, therefore, to produce by means of yeasts alone any liquor containing more than 14% of alcohol. Those wines which contain more (like port, with 17% or more) must be "fortified," that is, alcohol must be added to them; while whiskey, brandy, etc., are still more artificial, being distilled liquors.

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* Buchner, E. Alcoholische Gährung ohne Hefezellen. Ber. d. Deutsch. Chem. Gesellsch., 1897 and years following.

† *Loc. cit.* Bd. II. p. 160.

The souring of milk, the so-called lactic-acid fermentation, is due to the activity of a great number of aerobic and anaerobic organisms, especially bacteria. These ferment the sugars found in solution in milk, first inverting the sugar if necessary, then splitting it mainly into lactic acid, thus—

$$C_6 H_{12} O_6 = 2 C_3 H_6 O_3$$

but producing also, in proportions characteristic of the species, acetic, formic, and other organic acids, and carbon-dioxide. Since these organisms can be active in the presence of only a comparatively small amount of free acid, only a small part of the available sugar is, under natural conditions, fermented by them. If, however, the free acid be neutralized by the addition of calcic-carbonate to the milk, fermentation will be resumed and continued until again an excess of free acid accumulates. The addition of lime-water (a dilute solution of calcic hydrate) to the milk given to infants is advantageous because it neutralizes the traces of free acid which may have been formed in the milk.

Butter becomes rancid when the obligate aerobic and the facultative or obligate anaerobic bacteria invariably present in butter succeed in decomposing the dextrose and other non-nitrogenous substances, possibly also some of the proteids, into a number of simpler compounds of which butyric acid is the most abundant and characteristic. The by-products, gaseous and other, odorous or not, vary with the organisms accomplishing the fermentation, while the substances acted upon, the course of the reactions, and the activity of the fermentation vary also with the conditions.

It must not be inferred that all so-called fermentations are the result of splitting the compounds acted upon into simpler ones. The acetic acid fermentation, for example, is an oxidation carried on by aerobic bacteria (two species, according to Hansen,* *Bacterium aceti*, *B. Pasteurianum*), although, as we have seen, acetic acid is a common by-product in anaerobic fermentations. Acetic acid is produced on a commercial scale either by destructive distillation of wood, or by the slow oxidation of dilute solutions of alcohol in the presence of free oxygen (*i. e.* in the air) by living organisms. The optimum temperature for these (20–30° C.) is lower than the optimum for alcoholic (25–30° C.), butyric (35° C.), and lactic (45–50° C.) fermentations, and they can withstand a decidedly higher amount (8–14%) of free acid than most other organisms.* So long as the acetic bacteria are adequately supplied with alcohol for respiration, they continue to form acetic acid to the amount above indicated; but if the supply of alcohol is insufficient, they oxidize some of the acetic acid, setting free carbon-dioxide, which is not produced under favorable conditions.

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* **Hansen.** *Loc. cit.*

Besides these fermentations, which are carried on in solutions by specific organisms, there are similar processes carried on in the living body by specific parasitic organisms, mainly bacteria, which liberate the energy and supply themselves with the food which they need by attacking either the living substance of the body itself or the lifeless food-substances enclosed within its cells. The main and the by-products of these parasitic organisms cause the systematic disturbances of the functions of the host organism, which are characteristic of the different forms of disease. So, for instance, the bacillus of diphtheria (*Bacillus diphtheriæ, K-L.*) causes decompositions in the limited area of the mucous membrane of the throat, which it commonly attacks, and the products of these decompositions, poisons, diffusing through the body of the host, are the direct causes of the disease rather than the presence, merely locally irritating, of the parasitic organisms. This discovery, that the poisonous products of the specific bacteria of disease, and not the bacteria themselves, are the direct causes of disease, has opened a new chapter in the science of medicine; but so long as our knowledge of the chemistry of these products, and of the processes which result in their formation, lags behind our knowledge of the organisms themselves, the treatment of the germ-diseases must continue to be largely a groping in the dark.

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* *Citromyces*, according to Wehmer (Beiträge z. Kenntnis einheimischer Pilze. I), can withstand successfully at least 20% of the citric acid which it forms from sugars.

In addition to those fermentations or decompositions accomplished in the living body or in lifeless substances by distinct species of organisms, there are other equally profound chemical disturbances which are due to the combined activities of organisms of more than one species. In the comparatively simple case of the so-called nitrogen bacteria one species decomposes and converts ammonia salts into those of nitrous acid, and another these nitrous salts into nitric. Many other decompositions taking place in nature are the result of the co-operation of several or many species of organisms, some anaerobic, others aerobic, the former preparing the way for the latter. The final products and all the intermediate ones will vary according to the organisms co-operating. The simplest, though not necessarily the mildest, diseases are due to the activity of single species of organisms. The simplest fermentations are the same. Both are decompositions, with or without oxygen. The more complicated diseases are those due to mixed infections, in which two or more species act together. The one species makes life easier for the other, the products of the one furnish food or the sources of energy for the other, the main or the by-products of both supplement each other by weakening the host. Typhoid-malaria, and even the mild protective disease which is the result of vaccination, are mixed infections due to the co-operation of two or more (probably three or four) species, no one of which alone is able to produce the disease.

We have then in nature a series of chemical decompositions accomplished by living organisms, animals and plants, for the liberation of needed kinetic energy, and resulting in successive simplifications from the most complex compounds to the simplest—carbon-dioxide, ammonia, and water. The normal or aerobic respiration of all higher and most lower organisms results in the direct destruction by oxidation of the most complex compounds. Anaerobic or intramolecular respiration, fermentation, decay, and disease, attacking the same complex compounds first, result in the formation of the same simple ones finally. This is done only slowly, through many stages, with the same total of released energy, but with far less energy available for the individual organisms in the long chain. Thus the energy stored in the compounds elaborated by living organisms is set free again before and after their death, either by their own activity or by the activity of others. This energy becomes available for the construction of new energy-storing compounds, for work of the utmost physiological variety.

From the foregoing discussion it is evident that respiration, whether aerobic or anaerobic, is a process most intimately connected with the other functions of the living organism; a process dependent in the first place upon a supply of respirable (oxidizable or otherwise decomposable) material; a process which goes on, when once respirable material is adequately supplied, actively or tardily, according to the activity of the other functions, in other words, according to the demand for energy to do work. In the healthy organism, under natural conditions, the rate of respiration will equal the demand for energy; it will not exceed the demand, for stimulating respiration results in stimulating the other activities; it will not be less than the demand, for decreasing respiration decreases the amount of energy available for the other activities. The rate of respiration is controlled by the living cell, and whatever influences affect the total amount of energy demanded by it will also affect the rate of respiration, increasing or depressing the rate accordingly.

Respiration has no optimum temperature, no optimum illumination, of its own; it will increase or decrease with changes in temperature and illumination only as these affect the demand for energy on the part of the organism. Nutrient and poisonous substances and the amount of water will affect respiration only as they affect the organism. Injuries* cause a change in the rate of respiration, but they do so only by changing the demand for energy. To repair an injury or to close a wound new cell-walls must be deposited, new cells must be formed, more food must be manufactured, or stored food must be dissolved, the food must be carried to the seat of the injury and used there, and other kinds of work must be done. For all this extra work extra energy must be supplied, and hence the rate of respiration must be increased. This increased rate shows itself in plants as in animals by the increased production of carbon-dioxide and by a rise in temperature (wound-fever). In parts and in organisms most rapidly growing the rate of respiration will be high, but growth is only one function and when it decreases other functions may become more active, keeping the demand for energy uniform, and hence the rate of respiration will not necessarily decrease with a decreasing growth-rate.

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* **Richards, H. M. The respiration of wounded plants. Annals of Botany, Vol. X., 1896.**

The rate of respiration varies with the total demand for energy, not with any one function. For instance, the rate of respiration and consequently the liberation of energy (heat) reach their maximum in the spathes of Aroids* after the parts have passed the period of most rapid growth; for, though the growth-rate diminishes, the various processes concerned in and stimulated by fertilization demand an equal or even greater amount of energy.

In normal respiration the volumes of oxygen fixed and of carbon-dioxide evolved are approximately equal. When this ratio is not obtained in an experiment, the difference is to be accounted for in one or more of the following ways. *First,* the ratio will vary with the amount of oxygen enclosed in the body of the organism at the beginning of the experiment. This oxygen will be used before more can be absorbed. *Second,* only so much of the carbon-dioxide evolved (exhaled) can be measured as is not absorbed, or does not remain enclosed, by the tissues, or, in the case of water-plants, is not dissolved in the water. *Third,* other substances than carbon-dioxide and water may be formed in respiration (*e. g.* organic acids, alcohol, etc.) and therefore the different amounts of these other products in different organisms will evidently affect the ratio between oxygen absorbed and carbon-dioxide given off. The ratio will be changed either by the greater absorption of oxygen for the oxidation of organic acids or by the smaller amount of carbon-dioxide produced when such incompletely oxidized by-products as alcohol are formed. *Finally*, every factor in the environment of the organism, its food, the influence of its neighbors, the weather, etc., will affect the ratio more or less by affecting the organism itself.

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* **See Pfeffer, Pflanzenphysiologie, Bd. II., p. 404, of the first edition.**

For the reasons made clear in the foregoing pages, the amount of carbon-dioxide exhaled is by no means an accurate index of the rate of respiration and of the amount of energy liberated, but taking this substance only, we may still make some interesting comparisons. For instance—* man exhales in 24 hours CO_2, equal to 1.2% of his body-weight; moulds exhale in 24 hours CO_2, equal to 6.0% of their body-weight; active bacteria exhale in 24 hours CO_2, equal to 200.0% of their body-weight. Organisms which, like man, have comparatively feeble respiratory power, must either, as he does, supply themselves with energy by external means or limit their activities to what they can themselves produce. Flying birds produce much larger amounts of carbon-dioxide and hence of energy than man, and upon the latter depends their ability to fly. The very important part taken by the moulds and bacteria in Nature is accounted for by their being able to supply themselves with such tremendous amounts of energy.

SUMMARY

Respiration, controlled and accomplished by living organisms, produces disturbances of equilibrium in the *living* substances of the organism; these disturbances give *impulses* to further molecular and atomic movements and to further *vital* activities; respiration transforms latent (potential) to active (kinetic) energy, and reduces the amounts of carbohydrates and fats, to a less degree also protoplasmic substances, in the body.

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* Pfeffer. Pflanzenphysiologie, Bd. I., p. 526. Engl. transl., vol. I., p. 522.

CHAPTER III

NUTRITION

FROM the preceding chapter we have learned that respiration is a destructive process consisting either in the breaking up of complex compounds into simpler ones, or in the physiological oxidation of various combustible substances. With the important exception of the nitrogen, sulphur, and iron bacteria, which derive their energy from simple compounds, all living organisms depend for their chief supply of energy upon complex compounds existing in nature only as the result of the constructive activities of living organisms. In the last chapter we assumed the presence of these complex compounds, examining only the means of deriving energy from them.

Energy is needed for construction, to do work. Only so much energy can be liberated by complete combustion or complete decomposition as was employed in construction. Theoretically just as much energy should be liberated in the combustion of a starch grain as was needed to make it, but the cell is not a perfect machine; not all the energy or power used goes into the finished product, some is expended in overcoming the internal resistance of the machine, some is radiated, or "lost" in other ways. There is waste of energy and of material in every machine, the product does not represent the total expenditure of material and energy. As it costs a certain amount of energy to keep an engine going without its doing any other work, and a larger amount to make it do work as well as go, so it costs a certain amount of energy to keep an organism alive and more to make it do anything. The sum of the energy expended in making the engine go, plus the amount expended in making it do work, equals the amount of energy which must be developed to run it, if there is no loss by radiation, etc. So also the sum of the energy necessary to living, plus the energy necessary to action, equals the amount developed, provided there is no loss by radiation, etc. In the living organism this loss is less than in the machine; the organism is economical to a high degree.

With the exception of the bacteria mentioned (p. 40), all living organisms must have complex compounds, elaborated either by themselves or by other living organisms, from which to derive the energy which they need to continue living and to carry on their various forms of activity. These complex compounds are elaborated from simple ones. Owing to the discrepancy existing, even in the most economical organism, between the amount of kinetic energy required to elaborate a complex compound and the amount of kinetic energy which can be liberated from it, the organism cannot supply itself by respiration alone with sufficient energy to elaborate all the compounds it needs. It must acquire energy from outside of itself. This the majority of organisms do by taking into their bodies more food than they incorporate. Some of this food is destroyed to furnish energy for the elaboration, assimilation, and incorporation of the remainder.

Obviously this system cannot prevail throughout the whole series of living organisms. Some must obtain energy from a source entirely independent of organic life. This source is the sun, from which energy comes to the earth in the form of light. As will be shown more plainly later (pp. 55, 56), the sunlight is composed of radiant energy of at least three distinct sorts, of so-called heat, light, and chemical rays. Of these the light rays are the ones most used in making good the losses of energy due to living organisms not working with absolute economy. These rays are used to combine two of the food-materials concerned in the process of nutrition.

Nutrition consists in, 1st, the *absorption*, and 2d, the *combination* of *food-materials*, and 3d, the *assimilation*, and 4th, the *incorporation* of *foods*. Nutrition furnishes the materials for (*a*) supplying energy, (*b*) the construction of new parts, (*c*) the repair of worn parts. Every individual must sooner or later nourish itself, because food enough for continued living is not given to it by its parents in the seed, spore, or egg, or later.

THE FOOD-MATERIALS

The food-materials of all organisms are fundamentally alike. This conclusion may be formed from the observation that all animals are directly or indirectly dependent upon plants for food—the Carnivora preying upon the Herbivora, the Herbivora devouring plants. It might be suspected that the nitrogen, sulphur, and iron bacteria, peculiar in their sources of energy, might be peculiar in the foods used for the construction of their bodies. Chemical analysis of the bodies of all organisms, especially of the protoplasmic parts, shows that there are no exceptions. The conclusion above stated is further confirmed by culture experiments in which food-materials and foods of known composition are the only ones employed.

Analyses and cultures have shown that of the seventy or so chemical elements only ten are absolutely indispensable as food constituents, namely, carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, and iron. Two other elements are invariably found in analyses of the bodies of animals and plants, namely, sodium and chlorine, which are of universal occurrence combined as common salt. Only with the utmost difficulty is this compound excluded from cultures, and there may be doubt of its ever having been done. Owing to the universal presence of common salt, rather than because of its usefulness, it occurs in all organisms. Besides these twelve elements, others occur in more or less soluble compounds in the bodies of organisms. Some of these may be very useful though not indispensable. The composition of the soil or water in which plants live, will directly affect the composition of their bodies. Plants living in soils containing large quantities of copper, zinc, arsenic, aluminum, or silica will necessarily absorb larger amounts of the salts of these elements than plants living elsewhere. The plants containing most silica—the *Equisetums*, grasses, and sedges—employ this in stiffening their bodies; but they can successfully be brought to maturity without silica, although they will then be comparatively soft, mechanically weak, though physiologically vigorous.

From the few elements composing their food-materials plants manufacture foods of the utmost variety. These are present in the cells, either in solution or deposited in solid form. The foods may be divided into two groups according to the presence or absence of nitrogen as a component element. The non-nitrogenous foods are the ones first formed and the simpler—the sugars, starches, and oils; the nitrogenous foods are elaborated from the former and are more complex—the amides, proteids, nucleines, etc. Carbon, hydrogen, and oxygen are constituent elements of all the foods in both groups, and carbon must be considered the characteristic component element both of living organisms and of their food.

CARBON

The source of carbon for all organisms except the nitrogen bacteria and plants containing chlorophyll or its apparent equivalent physiologically, bacterio-purpurin, is, directly or indirectly, these color-containing plants. Since, however, the purple-bacteria play a comparatively unimportant rôle as food-producers, and their relations to carbon are like those of green plants, we need not consider them. The nitrogen bacteria will be discussed on page 68.

The direct source of carbon for green plants, the ultimate source for all organisms, is the carbon-dioxide of the air. This is proved by the following facts:* 1. Green plants cultivated in an atmosphere of normal composition, except that every trace of carbon-dioxide has been removed, soon cease to grow and finally die. 2. Green plants cultivated in a soil of otherwise normal composition, but containing no trace of carbon-compounds, thrive perfectly. 3. Green plants cultivated in water holding in solution the ordinary soil constituents except the carbon compounds, also thrive perfectly. 4. Submersed water plants cultivated in water containing all the usual salts, but no trace of carbon-dioxide, soon cease to grow and presently die. The second and third of these experiments demonstrate the error in the old theory and in the present popular belief that leaf-mould, loam, manures, and fertilizers, natural and artificial, are valuable because of their carbon content. Besides the phosphates which they contain, it is probable that the only valuable constituents are the nitrates.

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* For details as to experiments demonstrating these facts consult Darwin and Acton's Practical Physiology of Plants, Moor's translation of Detmer's, and the more recent "Laboratory Course in Plant Physiology" by Ganong, and "Practical Text-book of Plant Physiology" by MacDougal.

Carbon-dioxide forms about five-hundredths of one per cent. of normally pure air (.05%). From this we can calculate the percentage of carbon thus:

$$\begin{array}{lrl} \text{Atomic weight of carbon} = 12 & C & = 12 \\ \text{`` \quad `` \quad `` oxygen} = 16 & O_2 & = 32 \\ \hline & CO_2 & = 44 \end{array}$$

$$\frac{C}{CO_2} = \frac{12}{44} = \frac{3}{11}$$

$$CO_2 = .05\% \text{ of air.}$$

$$C = .05 \div \tfrac{3}{11} = .0135+$$

$$\therefore C = .01\% \text{ of air.}$$

From figures given by Noll* we can calculate the volume of air necessary to furnish the carbon contained in a tree weighing 11,000 pounds dry and 50% of the dry weight of which (5,500 lbs. = 2,500 Kilos) is carbon. Thus:

10,000 litres of air contain 5 litres of CO_2
5 " " CO_2 weigh 10 gr.
of this C weighs $\frac{1}{5}$ = 2 gr.
$\therefore$ 5,000 litres of air contain 1 gr. of C.
2,500 Kilos = 2,500,000 grs.

$$\begin{aligned} \therefore 2{,}500{,}000 \times 5{,}000 &= 12{,}500{,}000{,}000 \text{ litres} \\ &= 12{,}500{,}000 \text{ cubic metres} \\ &= 16{,}125{,}000 \text{ `` \quad yards} \end{aligned}$$

Hence 16,125,000 cubic yards of air must have their carbon-dioxide wholly extracted to supply the tree. Does a line drawn through the periphery of a tree weighing 11,000 pounds when dry enclose this volume of air? Certainly not, but this is immaterial, for the air is constantly in motion, agitated by mechanical means and by the winds. Furthermore, the air, a mixture of gases, is subject to the laws of diffusion of gases. The absorption or decomposition of one volume of any gas in a mixture will produce a diffusion current of that gas to make good the loss. Hence the tree, whenever it is absorbing carbon-dioxide, is the centre toward which numberless diffusion currents of carbon-dioxide molecules are moving. The rapidity of their movement is directly proportional to the rapidity of the absorption.

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* **Text-book of Botany, by Strasburger, Noll, Schenck, Schimper, translated by Porter, p. 196. New York, 1898.**

Noll's figures, giving the amount of carbon contained in a tree and the volume of air required to furnish this, may well be supplemented by Brown's figures of the hourly absorption of carbon-dioxide.* According to Brown's determinations there is an increase of one gram of dry substance (mainly carbohydrates) to every square meter of leaf surface of *Catalpa bignonioides* per daylight hour. To form

1 gr.	starch	1.628 gr.	CO_2 must be absorbed
1 "	glucose	1.466 "	" " " "
1 "	saccharose	1.543 "	" " " "

From these data 1.545 gr. of carbon-dioxide may be taken as the mean amount needed to form one gram of carbohydrate. This at normal temperature and pressure equals 784 cubic centimetres of carbon-dioxide, the volume of carbon-dioxide absorbed per hour by each square meter of leaf surface. If we take into consideration the fact that stomata occur only on the under side of *Catalpa* leaves, and that they occupy only 1% of the total leaf surface, we see that the absorbent power of the leaf is very great.

The daily absorption of such large volumes of carbon-dioxide from the air suggests the query as to the means of maintaining the supply. We have already seen that the respiration of plants and animals returns to the air, in the form of carbon-dioxide, all of the carbon contained in the compounds physiologically oxidized. In ordinary combustion also the carbon of the material burned returns to the air as carbon-dioxide. The subterranean fires that vent themselves in volcanic activity pour into the atmosphere very considerable quantities of carbon-dioxide. In these three ways the present proportion of cabron-dioxide in the atmosphere is maintained.

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* **Brown, H. T. The fixation of carbon by plants. Address to Chemical Section, Brit. Assoc. Adv. Science, 1899. Published in Nature, Sept. 14, 1899.**

The enormous deposits of coal and the accumulations of petroleum and natural gas suggest the hypothesis that in past geologic times the earth's atmosphere contained a higher percentage of carbon· than now. It is objected to this hypothesis that the animals of the Carboniferous Period, the time of greatest coal deposition, could not live in air so poisonous as to furnish carbon enough for these deposits. This objection does not appeal with especial force to physiologists. It by no means necessarily follows from the inability of the living relatives of the animals of the Carboniferous Period to withstand a high percentage of carbon-dioxide in the air, that the earlier animals were equally sensit ve. Probably the animals of the Carboniferous Period could no more exist under the conditions now prevailing, than their nearest living relatives could survive the conditions of the Carboniferous, no matter how like or how different might be the percentages of carbon in the air then and now. Furthermore, there is at least a suggestion, though not evidence, of a difference between the respiratory and other functions of the organisms of the Carboniferous and those of to-day in the fact that the nearest living relatives of the plants of the coal measures are the ones best able to survive high percentages of carbon-dioxide. By increasing the intensity of the light as well as the percentage of carbon-dioxide, ferns may be made to grow more rapidly than under the normal conditions of the present geologic age.*

For perfect understanding of the movements of gases we must engage in the study of physical chemistry. For us, however, who are studying only the elements of plant-physiology, the mention of a few of the simplest principles concerned, will sufficiently illuminate the subject. *First*, a vacuum cannot be produced adjacent to an unconfined volume of gas; the gas will flow, will be drawn, into the space whence gas is being removed in the attempt to form a vacuum. *Second*, the molecules of adjacent and unconfined volumes of gases of different compositions will move spontaneously until the gases are perfectly mixed. *Third*, the same molecular movement, which is called diffusion, will take place when gases of different composition are separated from one another by permeable substances. Most animal and vegetable membranes are permeable. If one gas consisting of oxygen and carbon-dioxide is separated only by a permeable membrane from another gas consisting of oxygen alone, carbon-dioxide will pass from the first through the membrane into the second until there are equal proportions of this gas on the two sides of the partition, and oxygen will pass from the second into the first until the proportion of oxygen to carbon-dioxide is the same in the two volumes. If for any reason (because of higher or lower temperature, for instance) the pressures of the two gases are unequal, diffusion of both gases will continue until the pressure becomes the same on both sides of the separating membrane. Diffusion tends, then, to equalize the pressures and to produce uniform composition in adjacent volumes of gases either unconfined or separated only by permeable substances.

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* See Pfeffer. Pflanzenphysiologie, Bd. I., pp. 310-15, Eng. Transl. I., p. 332.

Turning now to plants, we find that the simplest plants, consisting either of single cells or of cells in filaments or small masses, enclose gases by the permeable membranes bounding their cells. In higher plants, which consist of a larger number of cells in larger masses, the gases are not only enclosed within the cells by permeable membranes, but the spaces between the cells also contain gases. These spaces, and hence the volumes of gas which fill them, are continuous with the unconfined mixture of gases which forms the atmosphere. Any difference, therefore, between the composition of the mixture of gases filling the intercellular spaces and enclosed within the permeable membranes which bound the cells of plants and the atmospheric air outside will cause diffusion. This will tend to make the composition the same within and without the plant. But since every living active cell is constantly respiring, taking in oxygen and giving out carbon-dioxide, a difference in composition between the mixture of gases contained in the plant-body and the atmosphere is constantly brought about. As constant will be the diffusion currents, one inward consisting of oxygen molecules, one outward consisting of carbon-dioxide molecules. These currents, tending to restore the uniformity in composition, but never accomplishing this so long as the plant respires, prevent the undue accumulation of carbon-dioxide and maintain an adequate supply of oxygen.

Only in green plants, and in the green cells of these, is there any even apparent exception to this simple physical law. If, however, any cells which liberate carbon-dioxide in respiration also absorb and combine it again in food-manufacture, the diffusion currents to and from these cells will be made up of different molecules from those composing the diffusion currents maintained by other cells. In the green cells the process and the products of food-manufacture are the reverse of respiration, and the diffusion currents necessarily correspond. The green cells respire as constantly and at least as actively as other cells containing no chlorophyll; but while they are manufacturing food, they absorb and use more than all the carbon-dioxide which they exhale. Hence, in experimenting upon the respiration of green plants or of parts containing chlorophyll, it is necessary to stop the opposite and constructive process.

The absorption of carbon-dioxide gas is accomplished by means of the diffusion currents of this gas set and kept in motion by the combination of carbon-dioxide with water in the production of food. The absorption takes place through the walls of all the chlorophyll-containing cells of the lower plants. These are all small and for the most part aquatics. In *Fucus* and other large algæ periodically exposed to the air, there is a difference in the absorption to correspond with the division of labor among the tissues.

Cell-walls which are gelatinized or cutinized and infiltrated with waxy matters, as are those of the epidermal cells of *Fucus*, are less permeable to gases than are cellulose walls. Through the cryptostomata of *Fucus*, therefore, as well as through the stomata of higher land plants, the inward diffusion of carbon-dioxide is more rapid than through the walls of the epidermal cells.

For land-plants the value of the stomata as furnishing the gates through which the exchange of gases takes place, has been strikingly demonstrated by Stahl.* He shows that by smearing the stomata-bearing surface of leaves having stomata on one side only (usually the under side) with cocoa-butter or vaseline (neither of which is irritating), the absorption of carbon-dioxide, as indicated by the amount of starch formed, will be much less than when the gas can diffuse through both the open stomata and the more permeable walls of the epidermal cells of the stomata-bearing surface. If the epidermal cells of the upper surface of a leaf which has stomata only on the under and smeared side are injured by a cut or scratch just deep enough to penetrate the wall, the much more rapid diffusion of carbon-dioxide through the cut into the leaf than through the walls of uninjured epidermal cells will be shown by the greater quantity of starch formed in the chlorophyll-containing cells adjacent to the cut. In green land-plants the absorption of carbon-dioxide into the intercellular spaces is accomplished by the free inward diffusion of the gas, a diffusion which is controlled by the stomata, which can open or close as occasion demands. From these intercellular spaces the green cells absorb what carbon-dioxide they need through their permeable cellulose walls, just as the lower algæ absorb all their food-materials through their permeable cell-walls.

As we have already seen (p. 45), the volume of carbon-dioxide absorbed implies the very considerable absorbent power of the leaf, but when we recall how small a proportion of the leaf surface (*e. g.* 1% in *Catalpa bignonioides*) can be opened for the free diffusion of gases, we see that the absorbent power of leaves is still greater. According to Brown's measurements it is fifty times that of a strong potassic hydrate solution of equal surface.* That the diffusion will keep pace with this absorption is conceivable when it is known that the rate of diffusion through an opening one millimeter in diameter is forty times as fast as through an opening ninety millimeters in diameter. The smaller the opening, within certain limits, the more rapid the diffusion through it. Hence the movement of carbon-dioxide molecules through the stomata of an insolated leaf must be very rapid.

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* **Stahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung, Bd. 52, 1894.**

The absorption of needed carbon-dioxide by green plants is accomplished, then, by purely physical means, by diffusion. The continued absorption of carbon-dioxide, and of all other food-materials also, is accomplished by the same means; but in order that there should be continued absorption, continued inward diffusion, there must be continued removal of what is absorbed. If this were not so, there would presently result from the diffusion equal proportions of the food-materials within and without the plant, and the diffusion would then cease. The construction of foods out of the food-materials absorbed removes the food-materials, prevents their accumulating, and continues the absorption by maintaining the conditions for diffusion.

If we now examine the conditions and the means necessary for the elaboration of carbon-dioxide, itself innutritious though a food-material, into nutritious matters or foods proper, we shall at the same time come more clearly to understand how it continues to be absorbed. The conditions and the means, besides the presence of carbon-dioxide, are warmth, water, light of definite composition, chlorophyll, and living protoplasm. Warmth is necessary mainly as one of the general conditions for life, for at any temperature at which protoplasmic activity is possible diffusion and chemical combination are also possible. Water is necessary, for its component atoms become chemically combined with the carbon atoms of the carbon-dioxide. Light rays of definite wave-lengths are the force employed by the living protoplasm to separate the carbon, hydrogen, and oxygen atoms and to reunite them into another and more complex molecule than either carbon-dioxide or water. Chlorophyll is the pigment which absorbs these light rays. Living protoplasm is the only agent yet known which can combine these two universally occurring and extremely stable compounds, carbon-dioxide and water, into food for living beings.

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* Brown, H. T. The fixation of carbon by plants. Nature, Sept. 14, 1899.

CHLOROPHYLL

Chlorophyll is a pigment, more properly a mixture of two or more pigments, of unknown chemical composition, probably nitrogenous, extremely unstable, lifeless, but enclosed in the living protoplasm, usually in definite living organs of the protoplasm called plastids or chromatophores. In the cells of the lowest algæ, the *Schizophyceæ,* the peripheral layers of protoplasm contain a mixture of blue and green pigments which give to them their peculiar blue-green or olive-green hue. Whatever may be the function of the blue pigment, soluble in cold water, it is accompanied by a green pigment, or a mixture of pigments which is green, of similar composition and the same functions as chlorophyll. Higher algæ consist of cells more differentiated in that the chlorophyll is confined to definite parts of the peripheral layers of protoplasm, in bodies possessed of denser structure than the rest of the protoplasm, apparently of a living framework between the parts of which the chlorophyll, as a dense and oily liquid, is enclosed. With further division of labor in the cell the size of the chromatophores is decreased, their numbers are increased, and the enclosed pigments become denser. By these means the effectiveness of the chromatophores themselves is increased, their smaller size admits of their moving about in the cell, thus enabling them to occupy different positions at different times, but at all times the most advantageous ones; at the same time, a smaller proportion of the cytoplasm is limited to the work of food-manufacture.

The chief physical characteristics of chlorophyll, which is probably made as well as contained in the chromatophores, are its complete insolubility in water, its ready solubility in alcohol, its fluorescence, and the absorption bands of its spectrum. By reason of its insolubility in water, it is possible to separate chlorophyll from the other pigments sometimes masking its presence in the cell—the blue of the *Schizophyceæ*, the brown of the *Phæophyceæ*, the red of the *Carpophyceæ*, and the red and purple coloring-matters often present in the cell-sap of higher plants.* Having extracted these pigments in cold water, alcohol may be used to dissolve the chlorophyll, which will certainly go into solution more rapidly, and possibly also with less chemical change, if the alcohol be applied hot. Besides the chlorophyll, this extract will contain other cell-contents soluble in alcohol and not removed by the water, notably the fats and oils. The alcoholic solution is ordinarily very unstable, for though it will retain its color for a few days if kept in the dark, the change in color, which begins at once, continuing only less rapidly than in the light, is evidence of chemical changes finally resulting in its complete destruction. From a freshly made alcoholic extract of chlorophyll at least two colored substances may be separated in solution. Benzine or gasoline shaken with an equal volume of the alcoholic extract will take up the chlorophyll-green proper, leaving a yellow pigment or pigments in solution in the alcohol. This will not secure a complete separation of the two, however, for some of the yellow pigment will remain in the benzine. This yellow pigment is usually called carotin. To separate chlorophyll-green in anything approaching purity is a difficult task. The extreme instability of the pigments enclosed in the chromatophores makes it almost certain that they will be acted on by the organic acids present in the cells and extracted with them. Furthermore, the solvents of chlorophyll (alcohol, ether, etc.) extract the fats and oils also. Although many attempts have been made to isolate chlorophyll none has yet been really successful.*

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* Molisch, H. Das Phycoerythrin, seine Krystallisirbarkeit und chemische Natur. Bot. Zeitung. Bd. 52. 1894. Das Phycocyan, ein krystallisirbarer Eiweisskörper. *Ibid.*, Bd. 54, 1895.

The fluorescent quality of chlorophyll, more evident in its solutions than in the leaf, is revealed by the blood-red color visible when light is reflected from it. However, the physiological significance of this fluorescence is not understood.

The spectrum of a fresh alcoholic solution of chlorophyll is essentially the same as that of chlorophyll in the uninjured leaf. The spectra vary in any case with the density of the solution, the thickness of the layer through which the light passes, whether of solution or of uninjured tissue, and also with the plants examined. The different shades of green leaves similarly exposed to light, the differences in their spectra, and in the spectra of solutions derived from them, and the different substances obtained in the chemical examination of chlorophyll solutions from different species of plants, all point to there being at least different proportions of the component pigments of the mixture called chlorophyll, if not different pigments in the chlorophyll of different plants. Though the function of chlorophyll—the absorption of energy in the form of light rays—is the same in all green plants, it by no means follows that the chlorophyll of all plants is equally efficient in absorbing light rays or that exactly the same rays are used in all plants. Slight differences in the composition of chlorophyll would cause corresponding differences in the quality and in the quantity of the energy absorbed by it.

The spectra obtained from light which has passed through a leaf, and of alcoholic solutions of chlorophyll, are characterized by dark bands called "absorption bands," the broadest and darkest of which are between the lines B and C, and E and F, of the normal solar spectrum, that is, in the red, orange, and yellow, and in the green and blue parts respectively. In the normal solar spectrum are certain dark narrow lines, named after their discoverer, Fraunhofer's lines. These indicate parts of the spectrum in which there is no light or other known form of energy. When a chlorophyll screen is interposed in the path of a beam of sunlight the spectrum differs from that of normal light in that between the Fraunhofer lines B and C, and E and F, energy in the form of light has been absorbed by the chlorophyll. This energy, absorbed by the lifeless chlorophyll pigment, is what is employed by the living chloroplastid in elaborating a nutritious compound from carbon-dioxide and water. The accompanying figure indicates the absorption, as reported by Reinke,* of an alcoholic extract of green leaves, and of two leaves and of seven leaves of *Impatiens parviflora* interposed in the path of a beam of light.

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* The literature of the subject is voluminous. References to the older literature may be found in Monteverde's papers (Acta Horti Petropolitani, t. XIII., 1893); Kohl's (Bot. Centralbl., Bd. 73 *et seq.*, 1898); Bode's (*ibid.*, Bd. 77, 1899), and in an extended paper promised by Tswett, in his preliminary announcement in Bot. Centralbl., Bd. 81, 1900, also in a collective review by Czapek in Bot. Zeitung, II. Abth., May, 1900.

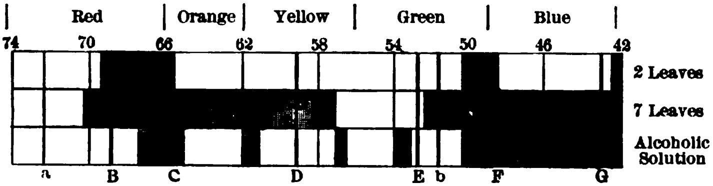

FIG. 1. CHLOROPHYLL SPECTRA. (AFTER REINKE.)

The figure shows plainly that light which has passed through one layer of chloroplastids is essentially and obviously poorer in energy than that which falls upon the first layer. The chromatophores of a single-celled green plant, and of plants consisting of filaments or single layered films of cells, receive beams of light containing the maximum of energy—assuming that none is absorbed by the medium in which they live. In plants composed of masses of cells, only the outermost layer of chlorophyll-containing cells receives the maximum amount of light and energy. The deeper layers evidently receive less and less. A moment's thought will lead one to conclude that only the peripheral layers of cells in a massive plant or organ will receive much utilizable light, and that flat organs like leaves cannot profitably consist of many layers of chlorophyll-containing cells. Examination of plant parts and organs shows that chlorophyll is developed in greatest amount in the outermost layers of the parts exposed to light, *i. e.* in the outermost of the cortical parenchyma cells and in the uppermost of the mesophyll layers of the leaf. Ferns and other shade plants develop chloroplastids in the epidermal cells, but in plants growing in situations abundantly lighted, it is not necessary to dispose the chlorophyll in the cells of the exposed surfaces.

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* Reinke, J. Untersuchungen über die Einwirkung des Lichtes auf die Sauerstoffausscheidung der Pflanzen. 2te Mittheilung: Wirkung der einzelnen Strahlengattungen des Sonnenlichtes. Bot. Zeitung, 1884.

The effectiveness of chlorophyll as an absorber of needed energy is proved by the excessively small quantity which is adequate to the needs of the plant. According to the frequently quoted estimates made by Tschirch,* there are between 0.2 and 1.00 of a gram per square meter of leaf-surface, or, in *Ricinus*, about 0.1% of the chloroplastids is chlorophyll pigment, and in leaves 2–4% of the ash-free dry-substance, 1.75–3.50% of the total dry-substance, is chlorophyll. As might be expected from the small amount of chlorophyll, the amount of energy absorbed by the leaf bears only a small proportion to the total amount falling upon it as sunshine on a bright day. Brown† estimates that 600,000 calories per square meter fall on a sunflower leaf per hour on a bright August day in England—certainly more than this in many other parts of the world. Sunflower leaves under these conditions form 0.8 gram of carbohydrate per square meter per hour, which requires 3,200 calories or 0.5% of the available energy. In diffuse daylight the percentage of energy absorbed and used is more in proportion to the amount received. It would seem, then, that the chlorophyll apparatus is so adjusted as to make the most of the amount of light daily available rather than being most efficient only when the light is unusually strong.

The relative values, as sources of energy, of the rays composing sunlight are indicated by the proportions of the absorption bands of the chlorophyll spectrum, the largest and darkest being in the most luminous part of the spectrum, the next toward the actinic violet end. Sachs's classical experiment of cultivating plants behind colored screens—the one consisting of a layer 1.2–1.5 cm. thick of a saturated solution of potassic dichromate, which absorbs the blue and violet rays wholly, but allows the others to pass; and the other of a layer 1 cm. thick of a dark solution of cuprammonia, which absorbs only the red, orange, and yellow rays—shows that the luminous rays absorbed are used to elaborate about 90% (starch serving as the indicator) of the food first formed by the plant, while the more actinic rays yield only 5–7%. Thus the energy absorbed by chlorophyll as indicated by the two main absorption bands in the spectrum is made to produce 95–97% of all the carbon food compounds first formed in the plant. The remaining 5–3% are formed by the other visible rays absorbed. The thermal ultra-red rays and the actinic ultra-violet rays, although absorbed by the plant, are not used in manufacturing non-nitrogenous foods. Engelmann's bacteria method,[†] now almost as famous as Sachs's colored screens, though applicable only to small plants, affords much more delicate and exact evidence of the statements just made. The method consists in the employment of motile aerobic bacteria in conjunction with small green aquatic plants. Beneath the stage of the microscope a prism is so placed as to throw a short spectrum upon the object on the slide. Upon the slide, in a drop of water containing motile bacteria, is laid a filament of *Œdogonium*, *Spirogyra*, or some similar plant. Around those cells illuminated by the red, orange, and yellow rays, the bacteria will congregate in greatest numbers, there moving with the utmost activity. Around other illuminated cells also the bacteria will collect, but in much smaller

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* **Tschirch, A. Angewandte Pflanzenanatomie, p. 57 *et seq.*, 1889.**

† **Brown, H. T. The fixation of carbon by plants. Nature, Sept., 1899.**

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[*] **Sachs, J. von. Wirkungen farbigen Lichts auf Pflanzen. Gesammelte Abhandlungen, Bd. I., p. 261** *et seq.*

[†] **Engelmann, Th. W. Botanische Zeitung, 1882, 1883, 1884, 1886, 1887.** *Also* **Die Erscheinungsweise der Sauerstoffausscheidung chlorophyllhaltiger Zellen. Verhandl. d. Amsterdamer Academie, 1894.**

numbers and in numbers about equal in all the colors, though somewhat more in the green-blue.

That both living protoplasm and chlorophyll pigment are necessary is shown, on the one hand, by the ineffectiveness of plastids well developed but colorless, and, on the other, by the complete inability of chlorophyll solutions either themselves to liberate oxygen from carbon-dioxide in the light or to enable colorless plastids to do so. The energy needed must be absorbed by chlorophyll in direct contact with and enclosed in living protoplasm, otherwise both energy and chlorophyll are useless. Chlorophyll grains mechanically isolated from living cells continue for a time to absorb carbon-dioxide and to give off oxygen, as may be shown by motile aerobic bacteria.* But if such isolated plastids are so treated that they pass over into a state of anæsthesia, they no longer absorb carbon-dioxide, and liberate oxygen although they still absorb light rays. The living protoplasmic body of the plastids, together with the chlorophyll pigment contained in it, are the organs by which plants begin the manufacture and elaboration of their food. These organs are to a high degree independent of the other organs of the cell and of the cytoplasm itself, but not entirely so; they are still cell-organs.

For the formation of chlorophyll in cells which normally contain it two conditions may be mentioned as of special importance, namely, illumination and the presence of iron. Most plants fail to produce chlorophyll in darkness, although a larger number than was formerly supposed are now known to produce it regardless of the illumination. Among these may be mentioned the seedlings of conifers and maples. The influence of light on its formation in most plants must be regarded as a stimulus rather than a prerequisite, although the work of the chlorophyll pigment can be done only in the light. Then only is there energy to be absorbed, and the radiant energy, falling upon the cell, will stimulate it to develop a more effective absorbent than wall and cytoplasm afford. The action of iron also, since it is in all probability not a constituent element of the chlorophyll pigments, must be either that of a stimulant to the living protoplasm to form chlorophyll, or else in some purely non-vital way an assistant in the synthesis of these color-compounds. The former supposition seems more probable, but neither has any strong evidence in its favor. However, neither light nor iron will bring about the production of chlorophyll in cells which do not contain chromatophores as living organs. The cells of animals, fungi, and certain of the phanerogamic parasites and saprophytes, contain no chromatophores, no organs, therefore, capable of forming, containing, and using the chlorophyll pigments.

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* Ewart, A. J. Can isolated chloroplastids continue to assimilate? Bot. Centralblatt, Bd. 75, No. 2. 1898, and other papers there cited.

PHOTOSYNTHESIS

The absorption of carbon-dioxide and the combination of water with it by green plants have for years been misleadingly termed assimilation or carbon-assimilation. The word assimilation may much more correctly and significantly be applied to the working up, by the living organism, of substances already somewhat resembling in constitution the substance of the organism itself. The word really means *making like*. No organism can make carbon-dioxide and water like itself till it has combined them. The food formed by combining the two innutritious substances, carbon-dioxide and water, can be used directly only as fuel, for respiration. It must be modified, added to, elaborated, changed in various ways not yet understood, until it becomes chemically and physically like the component matters of the body of the organism. Combining carbon-dioxide and water is food-manufacture—a synthetic process; the modification of this food which makes it immediately available as constructive material is assimilation—not necessarily a synthetic process. Since, as we have seen, the energy by which the synthetic process is accomplished comes from the sun, the name *photosynthesis* has been proposed for it.

Besides the substances absorbed—carbon-dioxide and water—and the final products of the synthesis—starch or some equivalent—nothing is known of the chemistry of photosynthesis. Only the relative numbers of the atoms forming the starch molecule are known, and therefore it is customary to give either the minimum formula or to indicate by *n* that the starch molecule should be represented by some multiple, probably high, though still undetermined, of the minimum proportional formula. The proportional amounts of the end substances are indicated, therefore, by this equation

$$n\,(6\ CO_2 + 5\ H_2O) = n\,(C_6H_{10}O_5 + 6\ O_2)$$

Starch, though frequently termed the first *visible* product of photosynthesis, is not formed in all chlorophyll-containing cells (*e.g.* those of onion leaves), and should never be regarded as the *first* product of photosynthesis. The complexity of the starch molecule and the simplicity of the molecules of carbon-dioxide and water, indicated by their respective proportional formulæ and still more plainly by their structural formulæ,* make it extremely doubtful if even the commoner sugars are formed directly. These, because they are formed and remain in solution, can be recognized only by chemical means, while starch, a solid with a refractive index different from the other substances in the cell, is

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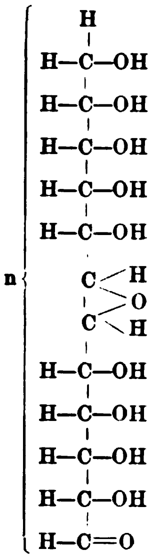
* The structural formula of CO_2 is probably $O = C = O$
" " " " H_2O " $H-O-H$
" " " " $n\,(C_6\,H_{10}\,O_5)$ may be



As examination of this structural formula shows, $C_6H_{10}O_5$ is only an approximate proportional formula for starch. It would be more correct to represent starch thus, $n\,(C_6\,H_{12}\,O_6)-(n-1)\,H_2O$. Evidently, the higher the multiple represented by n, the nearer this formula will come to the proportional $C_6\,H_{10}\,O_5$. These proportions were obtained by analysis. The exact numbers can be learned only by synthesis, and no one has yet been able to make starch.

visible as soon as formed, and it can be identified by the familiar blue-black color imparted to it by iodine.

In a very considerable number of plants and plant organs, starch is never formed, whether as the immediate product of photosynthesis or as food in store for future use. In these the food remains as sugars in solution, accumulates in visible form as drops of oil, or may be stored as reserve cellulose. It is in general true that in plants and in organs which, for any reason, should be especially light, oil separates instead of starch: *e. g.* in the Diatoms, most of which float either free or attached; in many of the *Phæophyceæ*, in the *Characeæ* (except the bulbils), and in such light and mechanically weak structures as the cylindrical leaves of onion, etc. The specific gravity of starch is higher, of oil lower, than that of water. Their nutritive values may be, probably are, about equal. Their values as sources of energy through respiration are not equal.* The advantage of oil as reserve food, or as the immediate product of photosynthesis, where lightness is important, is evident. Sugar never crystallizes in the cell, it remains always in solution, osmotically active (though comparatively weak), readily diffusible, and although occurring much more commonly as food immediately available or in transit from one part of the plant to another, it is sometimes the form in which food is accumulated and stored.

From considerations insufficiently supported by experiment upon the living plant, though based upon the relations of the members of the sugar group to one another, a series of equations suggesting the possible (some say probable) stages of the photosynthetic process has been proposed by organic chemists.* The following, proposed by von Baeyer, has much in its favor:

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* Complete oxidation (perfect respiration) of oil yields half again as many calories per gram-molecule as starch and sugar. See Chemiker Kalender where heat of combustion of vegetable oils is given, about 932 Cals while that of starch and sugar is about 709 Cals.

According to Stahl (Jahrb. f. wiss. Botanik, Bd. 34, p. 565, 1900), constantly submersed Chlorophyceæ, which run no risk of drying up during a period of vegetation, form starch, while on the other hand, those algæ subjected to frequent drying up form sugar. Water would evaporate less and less rapidly from a sugary or other solution of increasing density. The rate of evaporation would not be affected in any way by starch or other substances not in solution. *Vaucheria* and certain other algæ, some species of which are subject to drying up, contain oil in quantity. This cannot reduce the loss of water by evaporation. Are these algæ therefore less well protected against harm by drying, or is Stahl's conjecture a mistaken one?

$$CO_2 + H_2O = \underset{\text{(Formic Acid)}}{HCOOH} + O = \underset{\text{(Formic Aldehyde)}}{HCOH} + O_2$$

$$6n\,(HCOH) = \underset{\text{(Sugar)}}{n\,(C_6H_{12}O_6)} = \underset{\text{(Starch)}}{n\,(C_6H_{10}O_5} + H_2O)$$

To this series of reactions there are evident objections: *e. g.* formic acid and formic aldehyde are extremely poisonous, they cannot be formed free in the cell unless their conversion into harmless substances is instantaneous. The union of any of the alkaline elements with formic acid would imply the decomposition of the salts in which these elements enter the cell, namely, the phosphates, nitrates, sulphates, and chlorides. The decomposition of these salts, assuming that it could be immediately accomplished by formic acid or otherwise, would set free in the cell acids which, though less poisonous than formic acid, would still be injurious. To neutralize these another series of reactions would be necessary. Pursuing this theoretical discussion further along this line is unnecessary, for after all, assuming that the formic acid is neutralized by sodium, potassium, or any other element invariably present in combination in the cell, and that the reduction of this to an aldehyde takes place, the alkaline element must be eliminated to permit the condensation (polymerization) of formic aldehyde to sugar, and the element must be united again with some inorganic acid to form a harmless salt. There must, therefore, be at least one other series of reactions taking place simultaneously with the others.

Loew and Bokorny† have conducted experiments on *Spirogyra,* using as sole source of carbon a 0.1% solution of oxymethyl-sodium-sulphonate, which can readily be broken up at a regular rate into formic aldehyde and acid sodic sulphite. *Spirogyra* thrives on this diet, but this fact does not justify the conclusion of the experimenters that formic aldehyde is first formed or formed at all by green plants in the photosynthesis of food; it simply proves that *Spirogyra* is able under the conditions of the experiment to supply itself with carbon from other than the usual source.

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* Baeyer, A. von. Über die Wasserentziehung und ihre Bedeutung für das Pflanzenleben und die Gährung. Berichte d. Deutch. Chemischen Gesellsch., Bd. III., 1870. Fischer, E. Synthesen in der Zuckergruppe I. *ibid.*, Bd. XXIII., 1890. II. *ibid.*, Bd. XXVII., 1894.

† Loew, O. Ernährung von Pflanzenzellen mit Formaldehyd. Botan. Centralblatt, Bd. XLIV., p. 315+. 1890. Bokorny, Th. Über Stärke-

Emil Fischer's hypothesis regarding the formation of sugar (starch, etc.) by green plants,* represents the mature ideas of an eminent chemist; it is supported by no experimental evidence from physiologists, yet it is not out of place here. "The formation of sugar is accomplished, according to the plant-physiologists, in the chlorophyll grain, itself composed of optically active substances exclusively. I believe that the formation of a compound of carbon-dioxide or formic aldehyde with these precedes the formation of sugar, and that then the condensation to sugar, because of the asymmetry of the whole molecule, is accomplished asymmetrically. The elaborated sugar is torn away from the whole (chlorophyll) molecule and then used by the plant for the preparation of its other component organic compounds."

The elaboration of carbohydrates by the more or less indirect methods successfully followed by chemists, furnishes little more than plausible hypotheses as to how the green plant elaborates them. The chlorophyll apparatus is not identical in structure, probably much less in its operation, in all green plants, and it is not reasonable to suppose that the different substances formed by its operation are all elaborated in the same ways. Formic aldehyde may be an intermediate product in the formation of sugars and starch, and it may not; it is hard to see how it can be in the formation of fats and oils. Aided by the energy absorbed by the lifeless chlorophyll pigments, the living chloroplastids may form definite new molecules by uniting carbon-dioxide

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bildung aus Formaldehyd. Ber. d. Deutch. Bot. Gesellsch., Bd. IX., p. 103+, 1891, and Biologisches Centralblatt, Bd. XVII., 1897.

* Fischer, Emil. Synthesen in der Zuckergruppe, II. l. c., p. 3231.

or formic aldehyde with the already complex molecules of the pigments. By the same living agent, with or without solar energy, these molecules may be split into chlorophyll and sugar, but the chlorophyll pigments are so many that no one reaction or series of reactions will truthfully represent the process in all plants. The problem remains unsolved, and suggestive as the deductions of chemists are, its solution is to be expected from physiologists equipped with chemical knowledge rather than from chemists devoid of physiological experience.

In summing up this part of our study of the nutrition of plants, we may say that the non-nitrogenous foods, which first appear in the cells as sugars (cane and grape), mannit, etc., starch, fats, and oils, are formed from carbon-dioxide and water in the chromatophores (starch) or in the next adjacent cytoplasm (oil) by these living organs of the cell, the energy necessary for this synthetic process being absorbed by the lifeless chlorophyll pigments and used by the living protoplasm.

These non-nitrogenous foods accumulate temporarily in the plastids (starch), the cytoplasm (oil), and the cell-sap (sugars). The manufacture of these foods can be accomplished only during the hours when the plant can secure the necessary energy, *i. e.* while it is suitably illuminated. The removal of the manufactured product goes on independently of the illumination, for whenever the food is in soluble form and in solution, it will diffuse out of the cells in which it is made into others containing smaller amounts of these substances. This diffusion goes on constantly, the rate of diffusion varying only with the differences in the amounts of the foods in the different cells. While the plant is strongly illuminated, however, the rate of manufacture is higher than the rate of removal by diffusion, and the food accumulates at this time in the cells forming it. Hence, in the early morning, we may find the chlorophyll-containing cells free from starch, oil, and anything more than small amounts of sugar, at the close of the day, full of them. If, because of prolonged or too intense illumination or because of any other unusual circumstance, the rate of manufacture exceeds the rate of removal in twenty-four hours, there will be an increasing excess of food in the chlorophyll-containing tissues. If this continues for a number of days, the leaves will become filled with accumulated starch, etc., will become abnormally heavy, and by their unusual plumpness, difference in color, etc., will give evidence of their morbid condition. Such "fatness" of leaves is sometimes found in nature, more frequently, however, in cultivation. The cure is easy: shading the plants will reduce the rate of food manufacture and permit the nightly emptying of the daily filled cells.

When food is deposited in indiffusible form in any cell, it must be dissolved before it can be removed. Water is invariably the vehicle of food substances in the plant as in the animal body, and the foods are carried from cell to cell only in solution. Starch grains, deposited either in the chloroplastids, in which the carbohydrate is formed, or in the adjacent cytoplasm, must be converted into sugar and dissolved before they can be removed. In the chlorophyll-containing cells which manufacture food in the light and accumulate the manufactured product in the form of starch, diastase or some similar starch-converting enzym must be present in the green tissues of leaves, and in other chlorophyll-containing parts. To demonstrate its presence, however evident its effects may be, is difficult, because of the very small amount required to do the work in the time allowed the plant. To convert a large amount of starch quickly into sugar, a comparatively large amount of diastase is needed. If the time be longer, less diastase will do the same work. Its converting power is astonishingly great —10,000 times its own weight of starch.* The removal of food goes on constantly. Its manufacture is only periodic. A small amount of diastase secreted by the cell will therefore accomplish, in the twenty-four hours, the removal of all the starch normally deposited in the cell as the result of photosynthetic activity. That diastase is formed in small quantities in green leaves is indicated by the investigations of Vines.†

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* Schleichert, F. Das diastatische Ferment der Pflanzen. Halle, 1893.

† Vines, S. H. On the presence of a diastatic ferment in green leaves. sAnnals of Botany, V., 1891.

The products of photosynthetic activity are, as we have seen, food, water, and oxygen. These, in obedience to the laws of diffusion, pass out of the cells in which they are formed into others which contain less, or into the air. The oxygen set free may be used in part in respiration, but only a small part of the considerable quantity of oxygen liberated in active photosynthesis can be respired during that time by the plant producing it. The volume of oxygen given off during the life-time of a plant will equal that of the carbon-dioxide absorbed, for respiration and photosynthesis balance each other. As the volume of carbon-dioxide given off may be used as a quantitative index of the respiratory activity, so the volume of oxygen may be used as a quantitative index of the photosynthetic activity; but for reasons corresponding to those discussed under Respiration (pp. 38, 39), these indices are not exact. Both gases are at the same time concerned in other processes besides those which we have so far separately examined. The accompanying figure shows the relative activity of photosynthesis and respiration as indicated by the volumes of CO_2 concerned.

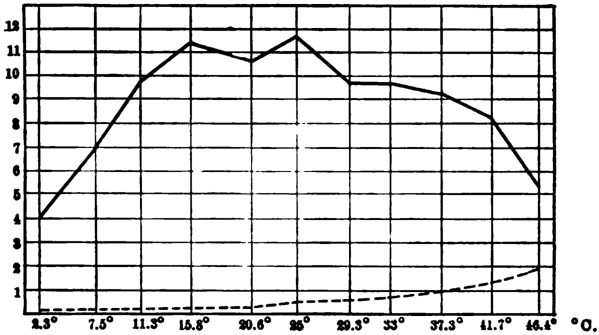

Figure 2.—Photosynthesis and respiration of a leafy branch of *Rubus fruticosus* (after Kreusler*). During photosynthesis the branch was in air containing 0.3% CO_2, and was illuminated with electric light approximately equal to the diffuse sunlight. The upper curve indicates the amount of CO_2 actually consumed in photosynthesis.

——CO_2 used in photosynthesis } per hour in each sq. dm. of
....CO_2 produced in respiration } leaf surface.

*** Copied by Pfeffer, Pflanzenphysiologie, Bd. I., p. 321. Eng. transl. I., p. 337, from Kreusler's paper in Landwirthschaftliches Jahrbuch, Bd. 16, 1887.**

The water liberated in the cell by the condensation of starch from sugar passes off in the ways to be discussed later in connection with the transfer of water (see p. 137).

The food formed is used by the cell which forms it and by the other cells of the plant, either immediately or later. As we have seen, the food accumulates temporarily, hence only small amounts are used immediately. What is removed is soon disposed of in one or more ways; *first,* it may be used at once to build cell-walls, or to furnish energy by being respired; *second,* it may be stored as reserve food in organs other than those that produced it; *third,* it may be still further elaborated, serving as the basis for the construction of nitrogenous food. This leads us from the relations of carbon in the nutrition of plants to those of nitrogen.

NITROGEN

Although as essential a constituent element of the living matter and therefore of the food of all organisms as carbon, nitrogen forms a much smaller percentage of the dry weight of plants, and its distribution in the body is much less uniform. Carbon is found in all the skeletal parts of the body of a plant as well as in the living matter of the cells. The cell-walls, containing no nitrogen, composed mainly of a cellulose or of some derivation of a cellulose, form the skeleton of the whole plant-body, of the dead as well as the living parts. On the other hand, nitrogenous compounds occur only in the living parts or as small remnants in parts formerly living. They are found as reserve foods in the cells and as the living constituents of the protoplasm.

The amounts and the distribution of nitrogen in the plant-body are indicated by the following table: *

In mushrooms	7.26%	N. in the dry weight
" lupin seeds	5.0%	" " " " "
" pea "	3.5%	" " " " "
" rye fruits	1.9%	" " " " "
" green leaves	3–5 %	" " " " "
" potato tubers	0.3 %	" " fresh condition.

*** Frank, A. B. Lehrbuch der Botanik, Bd. I., p. 563, 1892.**

These figures show plainly that where there is the greatest proportion of living cells there is also the greatest amount of nitrogen. Where living cells are most active, as in green leaves and at growing points, and where there is the greatest and most compact accumulation of stored food, as in some seeds, the larger part of the nitrogenous substance will be found. In many seeds, and in such places of storage as potato tubers, reserve food is accumulated mainly as starch, to be worked up into nitrogenous compounds only as needed.

Nitrogen occurs in nature in the uncombined state, forming nearly four-fifths of the earth's atmosphere, and also united into compounds of very different degrees of complexity, solubility, and availability. Some of the compounds are the results of the constructive activities of living organisms (see p. 71), others are the products of their waste or decay (see p. 36), and still others originate independently of living organisms. Some of the nitrogen compounds absorbed by plants contain carbon, others do not.

The forms in which nitrogen is obtained by the plant are, therefore, much more varied than are the sources of carbon. The supply of nitrogen compounds is also far less constant. At times plants may obtain from the air, as well as from the soil and from the water, simple compounds of nitrogen, such as ammonia and other gaseous substances, formed in the air only under electrical influences, or escaping into the air from terrestrial sources.

With the exception of certain bacteria, either free-living or associated with higher plants, no living organisms can use the free nitrogen so abundantly supplied to them in the air. They are absolutely dependent upon compounds of nitrogen. Animals obtain all their nitrogenous as well as non-nitrogenous foods from plants; most plants must obtain their nitrogenous food-materials in the form of nitrates. In the soil and in fresh and salt water there occur, besides various nitrates, other soluble nitrogen compounds, some entirely free from carbon, others united with it in more or less complex forms. Substances of the latter sort are the constituents or the derivatives of animal excreta or of the dead bodies of animals and plants. These serve as the foods or as the food-materials of plants of various degrees of dependence, *e. g.* certain species of orchids, the so-called saprophytes, etc. Plants of this sort we shall consider later (pp. 78–92).

The main source of nitrogen for independent plants, that is, for plants which contain chlorophyll and which by means of it elaborate their own non-nitrogenous foods, is the salts of nitric acid, which are found in the soil and in water. The origin of these compounds in the soil, once supposed to be purely chemical, has only recently been shown, by the brilliant researches of Winogradsky,* to be the result of the activity of micro-organisms universally present in soil. These organisms, bacteria of only a few species and of exceedingly small size, have been isolated and cultivated by Winogradsky. He found them to be of two sorts, strikingly different in their physiological activity. The one sort—to which Winogradsky gave the generic names *Nitrosococcus* and *Nitrosomonas*—oxidize ammonia compounds (*e. g.* ammonic sulphate $(NH_4)_2SO_4$) to nitrites, salts of nitrous acid. The other sort—belonging to a single genus, called by Winogradsky, *Nitrobacter*—oxidize these to nitrates, salts of nitric acid. In the soil there is no accumulation of nitrous acid or its salts, for they are as rapidly oxidized by *Nitrobacter* as they are formed by *Nitrosococcus* and *Nitrosomonas*. Furthermore, there accumulates no free nitric acid, for this is neutralized by the carbonates commonly present. These reactions may be represented in simplest form thus:

$$(NH_4)_2SO_4 + 3\ O_2 = 2\ HNO_2 + H_2SO_4 + 2\ H_2O$$
$$2\ HNO_2 + O_2 = 2\ HNO_3$$
$$2\ HNO_3 + K_2CO_3 = 2\ KNO_3 + CO_2 + H_2O$$

As already suggested (see p. 20), these nitrogen bacteria are strikingly different from all other known organisms. Though they obtain the carbon needed for food-manufacture directly from the air as carbon-dioxide, they elaborate this without chlorophyll or bacteriopurpurin (see

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* **Winogradsky, S. Recherches sur les organismes de la nitrification. Annales de l'Institut Pasteur, IV., V., 1889-91. Zur Mikrobiologie des Nitrifikationsprozesses. Centralblatt f. Bakteriologie, 2te Abth., II., 1897.**

p. 43) and without the aid of light, obtaining the requisite energy by the oxidations which they accomplish as aerobic organisms.* Unlike the purple-bacteria, the nitrogen bacteria play an obviously important part in nature, preparing from otherwise useless materials those compounds of nitrogen upon which the existence of all other organisms depends.

Like all other substances concerned in the nutrition of organisms, the nitrates are soluble and enter the body only in solution in water. The nitrates, especially potassic nitrate, which seems to be the most useful of these compounds, absorbed by the roots of land plants and through other organs of floating aquatic plants, are transferred by diffusion throughout the body. The elaboration of these into organic compounds can probably be accomplished by all living plant-cells, but in higher plants, in which division of labor is carried to a high degree, it is accomplished by some cells and not by all, very likely in the leaves and other green parts or in parts not far distant. The manufacture of nitrogenous foods is accomplished both in darkness and in the deeper tissues, and also in the light and in superficial tissues.† It is probable that light, and even certain rays of light, favor the elaboration of nitrogenous foods.‡ The action of light is presumably that of a stimulus; light is probably not the direct source of the energy used. The energy used may be wholly of chemical origin, the elaboration of nitrogenous foods taking place by purely chemosynthetic processes; or it may be furnished by the physiological oxidation (respiration) taking place in the cells in which the compounds are being formed.

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* Godlewski, E. Uber die Nitrification des Ammoniaks und die Kohlenstoffquellen bei der Ernährung der nitrificierenden Fermente. (Polish) Reviewed in Centralblatt f. Bakteriologie, 2te Abth., II., p. 458. Well summarized in Fischer's Vorlesungen über Bakterien, p. 103, Eng. trans. p. 106.

† Susuki, U. Über die Assimilation der Nitrate in Dunkelheit. Botan. Centralblatt, Bd. 75, p. 289, 1898. On the formation of proteids and the assimilation of nitrates by phænogams in the absence of light. Bulletin VIII., No. 5, Imperial University, College of Agriculture, Tokyo, 1898.

‡ Godlewski, E. Zur Kenntniss der Eiweissbildung aus Nitraten in der Pflanze. Anzeiger der Akademie d. Wissenschaften, Krakau, March, 1897. Laurent, E. Recherches experimentales sur l'assimilation de l'azote ammoniacal et de l'azotte nitrique par les plantes supérieures. Bulletin de l'Académie Royale de Belgique, t. 32, 1896. Palladine, W. Influence de la lumière sur la formation des matières protèiques actives et sur l'energie de la respiration des parties vertes des végétaux. Rev. gen. de Bot., t. XI., 1899. Jost, L. Die Stickstoffassimilation der grunen Pflanzen. Biol. Centralblatt, Bd. 20, 1900. (Review of subject, and a bibliography, to date.)

The nitrogenous foods are found in plants either in soluble or insoluble form. The soluble compounds are the only ones immediately useful. They can be transferred from cell to cell, they can be directly acted upon by the various chemical influences brought to bear upon them by the living cells, they can be assimilated—converted into substances like those composing the living substance—and when so elaborated and assimilated, they become a part of the living protoplasm. In soluble form they occur mainly as amides, of which asparagin is the most abundant and probably the most important. The amides are found in greatest abundance in parts where the formation and growth of new cells are most rapidly taking place, that is, in those parts which demand most food of non-nitrogenous and nitrogenous sorts for construction of new parts (cell-walls and protoplasm) and for energy. From analogy with the known behavior of the carbohydrates, and from experiment, it may be concluded that the amides are not elaborated in growing parts, but rather are transferred to them from parts where they have been elaborated from sugar and inorganic nitrogen compounds, or from parts where the already elaborated nitrogen compounds have been stored. These compounds are stored, in most cases, in insoluble forms (*e. g.* the proteids), corresponding in this physical quality with the starches and oils, and associated with them in the cells of the storing-tissues,—in the pith, medullary rays, the cortical and pith parenchyma of roots, tubers, and other underground parts, in seeds, and in spores.

The complex nitrogen compounds are very unstable and are doubtless subject in the plant to more or less constant destruction and reconstruction. The destruction of complex nitrogenous compounds does not result in the higher plants in the excretion of waste substances, as in the animals.

The plant operates more economically. From the simpler compounds formed by breaking down a highly complex organic nitrogen compound, the plant reconstructs, with the necessary additions, complex compounds of the same or similar sorts. In green plants there is nothing corresponding with the excretion of urea by higher animals, and the view long held that asparagin and other amides retained within the plant-body are useless substances, like the excrementitious matters cast off by higher animals, has been shown to be false. Although the amides are undoubtedly formed in plants in consequence of the breaking down of proteid compounds, they must be regarded as also representing one stage in the syntheses of proteids.* The greater economy of plants consists in their being able to use the amides, and probably also other and simpler substances, formed during the destruction of the molecules of proteids, whereas animals are obliged to cast off large quantities of highly elaborated nitrogenous substances.†

By means and through progressive syntheses not definitely known, and not necessarily the same in plants of different species, the inorganic nitrogen compounds (nitrates) occurring in soil and in water are elaborated, in the body of the plant, to complex compounds containing carbon, hydrogen, oxygen, and nitrogen. Amides, of which asparagin ($C_4H_8N_2O_3$) is the most familiar, are gradually built up from nitrates, ammonia compounds, etc., in the plant-body. The amides are soluble, diffusible foods; they may be moved from part to part of the plant as needed, and used in the synthesis of more complex organic nitrogenous compounds, the proteids, etc. Phosphorus and sulphur are subsequently added to these complex nitrogenous compounds. Substances finally are formed which possess the same physical and chemical structure and properties as those composing the living protoplasm.

The incorporation of these final compounds, which are at the summit of the series of constructive processes carried on by the plant, into the living protoplasm, results in making them parts of the living substance. These molecules, the building up of which we have tried to trace, do not themselves necessarily become alive when they are made parts of the living substance, and yet these molecules recently formed and others similar to them constitute the physical basis of life, the living protoplasm. The new molecules incorporated into and made parts of the living protoplasm are not given any new or peculiar vital force, *vis naturæ*, or any other occult power, but are so distributed in space, have such rate and amplitude of movement, that under the conditions prevailing in the cell—the conditions which make life possible anywhere—they behave as do the old and are as the old.

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* Schulze, E. Über den Umsatz der Eiweisstoffe in der lebenden Pflanze. Zeitschr. f. physiol. Chemie, Bd. 24. 1898.

† When I was a student in his laboratory, Strasburger once said to me: "Es ist nicht wie im Thierreich. Die Pflanzen machen nie dummes Zeug!"

The majority of chlorophyll-containing plants depend, as we have seen, upon nitrates for their supply of nitrogen. In the laboratory, ammonia salts and even ammonia vapor may be made to serve as the source of nitrogen, but in nature they are not the immediate source for green plants. Besides the nitrates and ammonia, animals and plants may obtain needed nitrogen from three sources, namely, (*a*) in the uncombined state from the air, (*b*) from its compounds in excrementitious matter of animals, and in dead bodies of animals and plants, (*c*) from its compounds in living bodies. The last two sources (*b* and *c*) are drawn upon by dependent organisms—animals and saprophytic and parasitic plants. The first is used by bacteria, living either by themselves in the soil or associated with higher plants in special outgrowths of their roots.

ROOT-TUBERCLE PLANTS

For centuries it has been the profitable practice of farmers to use leguminous crops to enrich impoverished soils. A worn-out field will more rapidly recover its fertility if sown to clover than if allowed to lie fallow. Sowing to clover and plowing the crop under will evidently enrich the soil more than mowing it and plowing the stubble under, but even the latter is better for the soil than sowing to grass and plowing the whole crop under.* Chemical analysis of soils originally alike show that that of a clover field gains in nitrogen as well as in carbon, while that of a grass field gains only in carbon. In other words, plowing a grass-crop under returns to the soil only what the plants took from it, *plus* the amount of carbon absorbed from the air. On the other hand, plowing a clover-crop under returns to the soil what the plants took from it, *plus* the amount of carbon absorbed from the air, and nitrogen. Where did the nitrogen come from? Obviously it could come only from the air.

If clover, pea, alfalfa, or other leguminous seed be sown in sterilized soil of known composition, no increase in nitrogen will be discovered on analyzing the soil after the crop has been turned under. These seeds sown in soil of exactly the same composition, unsterilized, but otherwise treated in the same way before and during cultivation, will yield a larger crop, which will be found to have added nitrogen to the soil. These seeds, sown in soil of the same composition, sterilized and then inoculated, either by the addition of a small quantity of unsterilized soil or of clear water first sterilized and then shaken with unsterilized soil, will produce a crop as large, and yield as large a gain of nitrogen in the soil, as those sown in unsterilized soil.

From these experiments† the only possible inference is that the micro-organisms of the soil, and not the leguminous plants alone, are effectively concerned in the increase in the nitrogen content of the soil. The effectiveness of the micro-organisms, however, may be of one of two sorts; either they may themselves absorb and elaborate the free nitrogen of the air, or they may stimulate the leguminous plants to do so. An acquaintance with the nature of their association with the leguminous plants and with the micro-organisms themselves is a necessary preliminary to an intelligent discussion of this question.

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* See Year Book of U. S. Dep't. Agriculture for 1897 and other publications of the national and state agricultural departments for statistics of relative values of different crops as "green manures" in adding to the available nitrogen content of soil.

† For details see Frank, A. B. Die Assimilation des freien Stickstoffs durch die Pflanzenwelt. Bot. Zeitung, Bd. 51, 1893, and elsewhere, to which references are given in this paper.

Also various papers in the Deutsche Landwirthschaftliche Presse,
" " " " " Landwirthschaftliches Jahrbuch,
" " " " " Annales Agronomiques,
" " " " " Year Book U. S. Department of Agriculture,
" " " " " Reports of " " " " "
" " " " " " " Agricultural Experiment Stations of different states, etc.

On the roots of leguminous plants* develop nodules of various sizes, smooth or convoluted. The roots of plants only a few weeks old begin to lose their even contour and uniform diameter, swellings occur at irregular intervals, and these increase in size very considerably until the plant fruits. These nodules or root-tubercles, white or rose-colored, are composed mainly of thin-walled parenchyma cells, enclosing small intercellular spaces, and directly adjoining the vascular tissues. Sections of young tubercles show large cells with dense, coarsely granular contents, which, on closer examination, fall under two distinct heads, —the protoplasm of the cells, and slender rods which prove to be living bacteria. In older tubercles many of the bacteria have enlarged and degenerated, are of irregular Y and T forms. In still older ones, the bacteria are dead. In other cells than those composing the tubercles no bacteria are to be found.† When the plant begins to fruit, the tubercles lose their plump and even appearance, become emptied and shrivelled. Their cells then contain only fragments of the deformed and dead *bacteroids* (as the "involution" or degenerate forms are called) and only a few intact and living rods. These last, set free in the soil by the complete breaking down of the walls of the tubercles, survive until the following season and then accomplish the infection of the roots of the new crop. Infection takes place through root-hairs attacked and entered by these bacteria.* The bacteria may be grown in artificial culture media inoculated from tubercles. In such cultures there is an appreciable increase in nitrogen.†

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* Also on those of alder (see Hiltner in Versuchsstationen, Bd. 46, 1896), *Eleagnus* (see Nobbe in Versuchsstationen, Bd. 41, 1892, and Bd. 45, 1894) and *Podocarpus* (see Janse in Annales du Jardin Botan. de Buitenzorg, Bd. 14, 1896).

† Contrary to Frank's assertion (Über die Pilzsymbiose der Leguminosen. Landwirthschaftliche Jahrbücher, Bd. 19, 1890), Zinnser (Über das Verhalten von Bakterien, insbesondere von Knöllchenbakterien, in lebenden pflanzlichen Geweben. Jahrb. f. wiss. Bot., Bd. 30, 1897) found bacteria in the tubercles exclusively.

Leguminous plants will grow in sterilized soil containing nitrates in forms and in quantities suitable for the successful cultivation of other plants, but under the conditions employed in experimenting they do not produce crops so good as when grown in unsterilized soil. The following figures will indicate the benefit they derive from association with the proper bacteria:‡

Per culture-jar, each holding two plants of *Lupinus luteus*—

I. WITH TUBERCLE FORMATION

Yield of dry substance in grams.	Weight of N therein.	Weight of N supplied in seed, soil, and water.	Gain or loss of N.
(*a*)38.919	0.998	0.022	+ 0.975
(*b*)33.755	0.981	0.023	+ 0.958

II. WITHOUT TUBERCLE FORMATION

Yield of dry substance in grams.	Weight of N therein.	Weight of N supplied in seed, soil, and water.	Gain or loss of N.
(*c*) 0.989	0.016	0.020	— 0.004
(*d*)0.828	0.011	0.022	— 0.009

(*d*) was watered with sterilized lupin-soil water (40 grams).

(*a* and *b*) watered with unsterilized lupin-soil water (40 grams).

(*c*) was watered with sterilized (tap ?) water.

It must be borne in mind, however, that though the leguminous plants may appear to profit by such association with bacteria, these results are derived from experiments under conditions wholly unnatural to all the plants experimented upon, and must therefore be taken with reserve. Leguminous plants grown in glass vessels undeniably do better when their roots are infected by bacteria than when their roots are sterile, but it has not been proved that leguminous plants do better with their roots infected than with sterile roots when they are grown where their roots can be properly aerated. Infected *Leguminosæ* benefit the soil more than do sterile ones, but what the gain to the plants themselves may be, remains to be shown, for the bacteria are plainly parasites.*

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* Peirce, G. J. Root-tubercles of Bur Clover and of some other leguminous plants. Proc. Cal. Acad. Sciences, Botany, vol. II., 1902.

† Mazé. Fixation de l'azotte libre par le bacille des nodosités des Legumineuses. Annales de l'Institut Pasteur, t. XI., 1897.

‡ Hellriegel und Wilfarth. Erfolgt die Assimilation des freien Stickstoffs durch die Leguminosen unter Mitwirkung niederer Organismen? Ber. d. Deutsch. Bot. Gesellschaft. Bd. VII., 1889.

The bacteria found in and causing the root-tubercles of the *Leguminosæ*, *Eleagnus*, etc., have not yet been isolated from the soil and are known only in the tubercles and in cultures inoculated from tubercles. The isolation of another species of bacteria which fix free atmospheric nitrogen (*Clostridium Pasteurianum*) has, however, been accomplished by Winogradsky.† Other species will doubtless be found in the cultivated and undisturbed soils of field and forest. The green and blue-green algæ growing on the soil were suspected of being able to fix uncombined nitrogen, but it has been demonstrated that they cannot do this alone.‡ It may be that nitrogen-fixing soil-bacteria and low algæ live together in an association similar to that of bacteria and leguminous plants.§

The number of organisms which can use free nitrogen will undoubtedly be found to be small, for in the present balance of nature little more nitrogen need be added to the soil than is yearly returned to it in the excrementitious matters and in the dead bodies which fall upon it. In these waste matters are organic nitrogen compounds upon which depends the existence of a very large number of organisms which break down these complex substances to simple nitrates, the nitrogen compounds which alone are useful to the majority of green plants.

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* Peirce, G. J. *Loc. cit.*

† Winogradsky, S. Sur l'assimilation de l'azote gazeux de l'atmosphère par les microbes. Comptes Rendus, t. 116, 1893, t. 118, 1894; also Archives des Sciences Biologiques St. Petersburg, Bd. 3, 1895.

‡ Kossowitsch, P. Untersuchungen über die Frage, ob die Algen freien Stickstoff assimiliren. Botanische Zeitung, 1894.

§ Pfeffer, W. Pflanzenphysiologie, Bd. I., p. 386. Engl. transl. I., p. 396. See also Krüger und Schneiderwind in Landw. Jahrb., Bd. 29, Nos. 4 and 5, pp. 771, 804 1900.

The organisms accomplishing these decompositions take into their own bodies nitrogenous and non-nitrogenous carbon compounds elaborated by other and higher organisms, reconstruct and assimilate some of the substance, making it a living part of themselves, decomposing the rest by physiological oxidation or by anaerobic respiration in order to obtain energy. In the farmer's manure pile there are countless dependent organisms which fall into separate species, easily conceivable but most difficult to isolate. On the surface of the pile are fungi and bacteria which respire aerobically and attack mainly the non-nitrogenous matters, the cellulose walls in the fragments of straw, and other vegetable remains. Within the pile are the anaerobic organisms, the first set living on the proteids and amides contained in the animal and vegetable matters, building up their own body substance from some of these and decomposing others. Living upon the decomposition products and upon the dead bodies of the first is the second set, which similarly build up and break down. A third set subsists on the products and upon the remains of the second; and so on down to the nitrite and nitrate bacteria which oxidize ammonia (the ultimate product of a great number of decompositions) to nitrites and these to nitrates respectively.

When the highly complex protoplasmic substances of animals and plants, upon which few organisms can live, are broken down to ammonia, water, carbon-dioxide, etc., and the ammonia is oxidized to nitric acid, green plants can begin again the constructive processes which end in the formation of living protoplasm from inorganic nitrogen compounds of the simplest sort. Thus we have the cycle of nitrogen in the physiology of living organisms.

A number of plants—some leading an apparently independent existence—are forced, or at least find it advantageous, to add to their supply of nitrogenous matters by taking into their bodies organic (that is, carbon) compounds of nitrogen. These plants fall into one of three classes,—the humus plants, the carnivorous plants, and the parasites.

HUMUS PLANTS

The humus plants live in soil containing a large amount of organic matter, mainly of vegetable origin, in a more or less decomposed condition. Besides these organic remains, living saprophytic fungi form an important constituent of humus. Owing to the very diverse composition of humus soils (loam, leaf-mould, etc.), it is very difficult to determine what substances are absorbed from them by plants, but since the majority of the humus plants contain either no chlorophyll or only a little, they must absorb elaborated non-nitrogenous, as well as nitrogenous, carbon compounds. These soils consist largely of substances insoluble or only slightly soluble in water. It is very probable, therefore, that there is a solvent action exerted by the underground parts of humus plants. The fact that even the immediately soluble constituents of humus soils diffuse only slowly, strengthens the supposition that some if not all of the humus plants dissolve the nutritious substances upon which their life depends. Those growing in humus soils containing little soluble food-material, but incapable of secreting acids or other solvents, depend upon other organisms which can exert a solvent action and with these they live in more or less intimate association.

The plants most active in converting the insoluble nitrogenous substances in lifeless remains of higher organisms into soluble and hence more generally available compounds, are, as we have seen, the bacteria. Almost equally important are the saprophytic fungi—toadstools and similar plants common in all sufficiently moist humus. These fungi and the bacteria, in nourishing themselves, prepare the materials needed and used by other humus plants growing with them. One step farther some of the higher humus plants go. Instead of living merely close to the lower humus organisms, upon the activities of which they are dependent, they come into actual contact with these, their roots becoming invested or even penetrated by them. These associations, described by Frank* most fully, are still too little understood to enable one to determine what parts are played by the members, or to decide whether the association is of mutual advantage or not.

The association of filamentous fungi with the roots of higher plants—called *Mycorhiza* by Frank*—is not confined to those poor in chlorophyll (*e. g. Neottia*) or devoid of it (*e. g. Monotropa*), but occurs also in a considerable number of green plants (*e. g.* many *Orchidaceæ, Ericaceæ, Cupuliferæ, Pinus,* etc.). This, coupled with the fact that so little is known of the chemistry of nutrition in these associations, renders it impossible to draw any general conclusions regarding the work accomplished by the fungi. Those closely investing and making felt-like sheaths over the roots of certain forest trees (*e. g.* beech and pine) cannot be supposed to furnish the larger member of the association with non-nitrogenous carbon compounds from the soil, for these it can elaborate in abundance in its own green leaves. Mineral salts and appropriate nitrogen compounds the fungus may supply, *first,* because of its ability, by reason of its smaller size, to branch more finely and spread more widely among the soil-particles than can the roots; *second,* because of its decomposing action upon insoluble nitrogenous remains in the soil; and *third,* because it may elaborate or oxidize the otherwise useless ammonia compounds.†

It is claimed that the fungi may be of additional advantage because roots invested by them branch more profusely than naked ones, and hence are intimately in contact with more soil particles and have a larger absorbing system.‡ Neither in this claim, nor in the observation that root-hairs are largely absent from the roots of green as well as other plants associated with Mycorhiza fungi, are there any grounds for assuming that we have other than pathological conditions due to the interference of the fungi with the normal independent habits of higher plants. So far as the chlorophyll-containing plants are concerned, Mycorhiza seems an affliction rather than a blessing, despite the claims of Frank and of Stahl. Frank says the growth of seedlings of beech and pine, cultivated in sterilized humus soil, is less than of other seedlings of the same sort in the same soil unsterilized. Stahl shows that plants ordinarily free from Mycorhiza grow better in sterilized than in unsterilized humus. It remains for experiment to show whether beech, pine, and other plants with fungi usually on or in their roots grow better in sterilized fertile soil free from humus or in humus which has not been sterilized. Some green plants are strictly humus plants, refusing to grow in other soils, but one cannot now conclude from this that they are dependent upon the fungi, rather than upon any other constituent of the humus. Sterilizing a humus soil causes changes in the physical and chemical conditions of many nitrogenous matters in the humus. Some plants are able to accommodate themselves to these changes, others are not. Sterilizing the humus causes the death, not only of the Mycorhiza fungi, but also of the nitrifying bacteria and of those other bacteria and fungi which directly or indirectly produce ammonia from the organic nitrogen compounds. These changes must profoundly disturb the balance of activities in the soil. It is, therefore, much easier to understand the benefit derived by the fungi from their intimate association with the roots of plants able to manufacture food for themselves, than to be convinced that the independent green plants greatly benefit by association with dependent ones. However, the subject deserves further investigation.

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* Frank, A. B. Lehrbuch der Botanik, Bd. I., 1892. Also Percy Groom in Annals of Botany, Vol. 9, 1895. See also Stahl, E. Der Sinn der Mycorhizenbildung. Jahrb. f. wiss. Bot., Bd. 34, 1900. MacDougal, D. T. Symbiotic saprophytism. Annals of Bot., XIII., 1899.

† Frank, A. B. Die Krankheiten der Pflanzen, 2te Aufl., 1895. Also die Bedeutung der Mycorhiza-Pilze für die gemeine Kiefer. Forstwissenschaftliches Centralblatt, XVI., 1894.

‡ Stahl, E. *Loc. cit.*

The association of high and low colorless plants in Mycorhiza is different only in degree, not in kind, from their simultaneous occurrence in all places where there are highly elaborated nitrogenous and non-nitrogenous materials. As the nitrate bacteria can work only upon nitrites formed from ammonia by the nitrite bacteria, and the sulphur bacteria can live only where sulphuretted hydrogen is abundantly set free either by organisms or in sulphur springs, so in the humus soils some organisms live upon the simpler products of their neighbors. It is easy to conceive that more than neighborhood nearness might be advantageous to some, and that these, gradually growing together, might form associations, mutually though perhaps not equally beneficial. The penetration of small organisms, or small parts of organisms, into and even through the living cells of others, is not necessarily fatal to the penetrated cells, as is shown by the symbiotic association of algæ enclosed in the cells of certain Infusoria, and even by some parasitic associations.*

In all of these cases, however, we have no new physiological principles. The nutrition is fundamentally the same, the food-materials are acquired and elaborated, the foods are assimilated and incorporated, in the same way in all organisms, although the sources of food may be different in different cases.

CARNIVOROUS PLANTS

The carnivorous plants have been exploited especially by "ecologists," students of the adaptations of plants to their surroundings, and their writings furnish the proper sources for more general information regarding them;† but the peculiarities of their nutrition are still within the province of pure physiology. These extraordinary plants may be divided into two classes: *first,* those which forcibly capture, and *second,* those which simply entrap, their prey. These classes may be represented respectively by *Dionæa,*

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* For example, the cases cited by De Bary (Morphology and Biology of the Fungi, Mycetozoa, and Bacteria, Eng. transl., p. 392, 3) and the survival of chlorophyll-containing cells of the host even when penetrated by cells from the haustoria of *Cuscuta* (Peirce, Annals of Botany, Vol. vii., p. 308, 1893).

† See Darwin's Insectivorous Plants, Goebel's Pflanzenbiologische Schilderungen (Insektivoren), Kerner and Oliver's Natural History of Plants (Vol. I., part I.), Cohn's Die Pflanze (Bd. II., Insektenfressende Pflanzen), Ludwig's Lehrbuch der Biologie der Pflanzen, etc., etc.

Drosera, *Pinguicula*, and by *Sarracenia*, *Darlingtonia*, the *Nepenthes*, and *Utricularia*. Of these *Drosera*, *Sarracenia*, and *Utricularia* are most familiar and will sufficiently illustrate the principles concerned.

Drosera, the "Sun-dew" of northern bogs, is a low annual, with nearly horizontally expanded, round, or elongated leaves, characterized by peculiar columnar outgrowths from the upper surface. The chlorophyll of the leaves is usually masked by the red cell-sap of the superficial cells and by the slender outgrowths. These last are multicellular, traversed for about half their length by a single vertical vascular bundle, and covered except on the top by ordinary epidermal cells with cutinized walls. The free ends of the columnar structures are enlarged and globular, glandular, and covered by a glistening, sticky, syrupy, more or less sweet secretion. Attracted by the unusual color and the glistening surface of these leaves, small insects alight upon them, taste the sweet secretion, and while they feed upon it are detained by its stickiness. The weight and movements of the insect induce movements in the hairs adjacent but untouched and in the blade of the leaf itself, as well as in the hairs with which it is in contact. Unless the insect is powerful enough to break away from the sticky surface, it presently comes into contact with other hairs and sticks to them also. Finally the blade of the leaf bends upward and the prey becomes enclosed between it and the many hair-like tentacles bending over upon it from all sides. The continued mechanical irritation of the hairs causes a more abundant secretion from the glandular ends; but, as Darwin has shown,* besides the mechanical there is also a chemical irritation, and this latter induces a change in the composition of the secretion. Non-nitrogenous material—a stone or a piece of wood—of similar size and weight will not induce the same response as an insect, a piece of meat or of hard-boiled egg, plainly showing that upon the chemical composition of the irritating body depends in part the nature of the irritation and of the response.

The continued contact of highly elaborated organic nitrogen compounds, largely proteids and insoluble, is followed by the secretion from the glandular ends of the hairs of a peptonizing enzym which attacks the nutritious substances and dissolves them. These solutions are absorbed into the plant through the cells secreting the enzym, diffuse from them into other cells, and are conducted away by the vascular bundle. After all the nutritious substances in the captured insect have been digested (dissolved) and absorbed, the leaf unrolls, again becomes flat, the tentacles loose their hold and become straight, the chitinous shell and the other useless remnants are exposed, dry, and blow away. The leaf is now ready to capture another insect. It is reported that each leaf has a digestive capacity for two or three flies.

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* **Darwin, Charles.** *L. c.*

When *Drosera* is able, by capturing and digesting insects, to supplement the nitrogenous food which it, like other plants, elaborates from the nitrates absorbed from the soil and the sugars made in its own leaves, it attains a larger size and produces more and better seeds (other things being equal) than when it must depend solely upon the complex nitrogenous foods made by itself.

It has been claimed by Tischutkin,* and the view has been somewhat generally accepted without due investigation, that the peptonizing enzym is secreted mainly, if not wholly, by bacteria symbiotically associated with *Drosera* on its tentacles, and not by the gland cells of the tentacles. There can be no question of the constant presence, under natural conditions, of bacteria on the tentacles, and it would be remarkable if there were none among these which formed a peptonizing enzym. However, these bacteria, peptonizing and other, are no more symbiotically associated with *Drosera* and no more concerned in the digestion of its insect food than the bacteria of the human mouth and digestive tract are symbiotically associated with man and aid in his digestive processes. In both cases we have to do with bacteria unavoidably and constantly, but also accidentally and

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*** Tischutkin, N. A Russian paper reviewed in Botan. Centralblatt. Bd. 50, p. 304+, 1892; also a later paper reviewed in Botan. Centralblatt. Bd. 53, p. 322, 1893.**

independently, present. They are not more intimately associated with the higher organism.

The same hypothesis has been extended to the digestion which takes place in the pitcher-like leaves of *Nepenthes*, and with much more justice to the decompositions in the similar leaves of *Sarracenia*. For *Nepenthes*, Goebel* and Vines† have proved the presence in the pitchers of an enzym capable of digesting proteid matters. Goebel ‡ says that the *Sarracenias* and *Darlingtonia* secrete neither an enzym nor a substance which checks decay; that is, they do not themselves digest the bodies of insects, but, on the other hand, they do not prevent the decomposition of these by living organisms contained in the pitchers. The *Sarracenias* and *Darlingtonia*, like *Drosera*, inhabit northern bogs, the soils of which are relatively poor in nitrogen. The leaves are large, erect or inclined, pitcher-shaped, holding often considerable volumes of water. Owing to the peculiar form, the slippery inner surface, and its downward-pointing hairs, the mouth of a pitcher is an alighting-place as uncertain as it is natural for flying insects. They fall down into the pitcher; their escape is prevented by the shape, slippery surface, and hairiness of the inside of the pitcher; finally they die, either by drowning, or of starvation and exhaustion from their futile efforts to get out. They now decay, bacteria feeding upon their dead bodies liberating soluble organic nitrogen compounds which are absorbed through the walls of the pitchers. If Goebel's conclusions, based on investigations carried on in the Botanic Garden at Marburg, are confirmed by equally reliable investigations of these plants in their native homes, they may constitute an interesting case of an association mutually beneficial; but it seems hardly a sufficient reason for the formation of such extremely modified leaves as these pitchers, that they serve only as traps for insects, culture-tubes for bacteria, and absorbers of the unused products of these micro-organisms. It would seem much more probable that, under their normal conditions, the walls of these pitchers, as of the *Nepenthes*, secrete an enzym which digests the bodies of entrapped insects. If this be true, the bacteria inevitably present do not aid the plant, they simply rob it of food which it can itself digest and afterwards absorb and assimilate.

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* **Goebel. K. Pflanzenbiologische Schilderungen. 2ter Theil. p. 186** *et seq.*

† **Vines, S. H. The proteolytic enzyme of Nepenthes. Annals of Botany, Vol. XI., 1897, Vol. XII., 1898.**

‡ **Goebel. K.** *L. c.*, **p. 170.**

Most of the *Utricularias* are aquatics, the peculiar submerged leaves of which entrap small crustaceans. It is still undetermined whether the crustaceans are killed and digested,* or whether they live on indefinitely. When they die naturally their bodies become decomposed by the water bacteria invariably present in the bladder-like leaves. At all events, the excreta, containing considerable quantities of organic nitrogenous matter, cannot fail to be directly or indirectly useful to the plant which harbors the animals producing them. The excreta may contain immediately available substances; the more refractory may first undergo chemical transformation by water-bacteria; finally the dead bodies and the lifeless excreta, falling a prey to bacterial activity, become available to the *Utricularia*, which profits accordingly.

PARASITES

A considerable number of plants of the most diverse sorts, from the simplest to the most highly developed, are able to live actively only upon or in the living bodies of other organisms. They may be able to survive in the resting condition entirely independently, but in this regard their seeds, spores, and cysts are like all others. For active vegetation they need their proper hosts. The relation of the parasite to the host is not in all cases simply that of the fed to the living organism which nourishes it. The host may do much more than supply the parasite with food: it may give it mechanical support, it may stimulate it to grow in characteristic forms, it may assist in the dissemination of its offspring, it may protect it in a variety of ways. In all of these respects the parasite is benefited.

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* Goebel K. *L. c.* p. 173.

In certain instances it is claimed that parasitism is advantageous not only to the parasite but also to the host. These cases must be examined separately. Pure parasitism is beneficial only to the parasite. Whatever may be our views as to the origin of parasitism, we must admit that parasitic associations are entered into each season only because the parasite is a dependent organism, incapable of elaborating its own complex foods from simple compounds. The parasite may be wholly dependent, taking from its host all the food it needs, or it may be only partly dependent, taking only certain kinds of food. In either case the foods absorbed are worked over, assimilated, incorporated or consumed, by the parasite itself. No food is absorbed by the parasite in forms which it can use without modification for building its own body.

The nutrition of parasites differs from that of other organisms only in certain stages of the process, and not fundamentally even in these. Instead of absorbing from water, soil, and air the raw materials which must be elaborated into foods, the parasite absorbs from its host matters already elaborated by its host. The means of absorption are the same in parasites as in other organisms (see Chapter IV.).

Parasitism consists essentially in the absorption from a living organism of more concentrated solutions of more highly elaborated food-materials or foods than can otherwise be obtained. Using the division of the process of nutrition proposed on page 41, into, *first*, the absorption, and *second*, the combination of food-materials, *third*, the assimilation, and *fourth*, the incorporation of foods, we see that the parasite differs from the self-sustaining and independent green plant only in omitting the second stage of the process, absorbing from its host the food-materials or foods already elaborated, which an independent plant would elaborate for itself. To make this clearer, let us examine a few instances.

Among higher plants, perhaps the simplest, in other words, the least complete form of parasitism is that of the European and American mistletoes, *Viscum album* and *Phoradendron villosum*. The mistletoes are green perennials containing in their leaves and in the cortex of the young and even older branches, an abundance of chlorophyll in normally effective chloroplastids. They are plants which can and do photosynthetically manufacture from water and carbon-dioxide all the non-nitrogenous food which they need. Elevated far above ground on the branches of oaks, poplars, apples, etc., they must draw from their hosts the water which they combine with the carbon-dioxide absorbed by their own leaves. Since the water in plants is a dilute solution of a large variety of matters, chiefly mineral, the mistletoe absorbs from its host these needed substances also. Their absorption is accomplished through peculiarly modified roots called *haustoria*, the wood or xylem elements of which connect directly with the wood elements of the vascular bundles of the host. Through the xylem the water absorbed from the soil and the mineral salts dissolved in it are transferred to the leaves. The mistletoe, tapping the water-conducting tissues of the host, establishes a water-conducting system continuous with that of the host, and so secures a supply of water and mineral salts as constant and as abundant as that of the host. On the other hand, the chief paths of transfer for elaborated foods, nitrogenous as well as non-nitrogenous, are furnished in higher plants by the phloem elements of the vascular bundles, but from these the foods are distributed osmotically through parenchyma cells to the tissues needing them. The phloem elements of the haustoria of *Viscum* and *Phoradendron* are not continuous with those of the host.* From this fact it has been inferred that mistletoe does not absorb elaborated foods of any sort from its host, that it is, therefore, only a "water parasite." This inference is scarcely defensible, though in the absence of direct evidence to the contrary the supposition is justified that *Viscum* robs its host of much less elaborated food than those parasites which have a direct phloem, as well as xylem, connection with their hosts.

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* Peirce, G. J. On the structure of the haustoria of some phanerogamic parasites. Annals of Botany, vol. VII., pp. 317, 318, 1893. Cannon, W. A. The anatomy of Phoradendron villosum, Nutt. Bull. Torrey Bot. Club, vol. 28, 1901.

Gaston Bonnier* claims that *Viscum* is sometimes directly beneficial to its host. In summer the host produces both actually and proportionally more food than the parasite, although the parasite is then photosynthetically active. At times during the winter and always during the early spring, when the host is leafless, the evergreen parasite may manufacture carbo-hydrates and the host cannot. While the host is not able to manufacture food and the parasite is, the host is alleged to draw upon the mistletoe for freshly manufactured non-nitrogenous food. It is, therefore, claimed by Bonnier that the mistletoe (*Viscum*) is parasitic either not at all or only very slightly, although obviously it obtains all its water and mineral salts from the host. But because the parenchyma tissues of the parasite are continuous through the haustoria with those of the host, furnishing the paths of osmotic transfer, the transfer taking place in one direction at one time may be in the opposite direction at another; and so it must be conceded, until proof to the contrary is adduced, that the mistletoe may be more than a "water parasite." Why should the host, on the warm days of winter and in the early spring, have any occasion to draw food from the mistletoe? A healthy apple-tree, or oak, or poplar, will normally lay by in its own body during the summer enough elaborated food to start it well in the succeeding spring. Upon this store it will draw promptly and satisfyingly when the need comes. Is there any less food stored in an apple-tree upon which mistletoe grows? If so, is not the mistletoe the cause, and can this lack ever be wholly compensated for? It would appear, then, that *Viscum* is a periodic rather than a partial parasite, and that only further investigation can show how nearly its indebtedness to its host is annually balanced.

Closer association with the host and greater dependence upon it are exhibited by the various species of *Cuscuta* or dodder, thread-like plants belonging to the Convolvulaceæ,

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***Bonnier, G. Assimilation du Gui comparée à celle du pommier. Actes du Congrès de 1889 d. l. Société Bot. de France: Bull. Soc. Bot. de France, 1890. Sur l'assimilation des plantes parasites à chlorophylle. Comptes Rendus, t. 113, p. 1074-6.**

but differing strikingly from the other members of the family in habit and habits. They are leafless twiners, yellow, orange, or even sometimes claret-red, in color, with very little if any chlorophyll. At frequent intervals their stems and branches form close coils around their hosts,* and from the inner surfaces of these coils haustoria grow into the tissues of the hosts. The haustoria have well-developed vascular bundles, the xylem and phloem of which are united, cell to cell, with the xylem and phloem of the adjacent vascular bundles in the host, thus perfectly connecting, in host and parasite, those tissues which conduct aqueous solutions of mineral salts and of elaborated foods respectively.† When the dodder has fastened upon a suitable host, sent haustoria into it, and connected its own vascular tissues with the corresponding ones of its host, it draws food in abundance. Chlorophyll develops only in smallest quantity in any part of it.‡ The dodder absorbs already elaborated all the sugars which it needs for the construction of cell-wall, for the supply of energy liberated by respiration, for the synthesis of amides, proteids, etc. Not having chlorophyll, it lacks the means by which to secure the energy needed for the elaboration of non-nitrogenous food, and for this food it depends wholly upon its host. Presumably it takes its nitrogenous food also in the soluble forms elaborated by its host, though it modifies, assimilates, and incorporates this for itself. When the dodder, having fastened upon an unsuitable host, is inadequately fed, it may become green by the formation of chlorophyll in the chromatophores always present in rudimentary condition in its cortical cells.§ It can thus add what it manufactures itself to the insufficient supply of non-nitrogenous food which it draws from its own innutritious host. The dodder makes food for itself only when it is unable to secure enough ready made.

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* See Chapter VI. for a discussion of the irritability of these and other plants.

† Peirce, G. J. *L. c.*

‡ *Ibid.*, A contribution to the physiology of the genus Cuscuta. Annals of Botany, vol. VIII., p. 91, 1894.

§ *Ibid.*, *L. c.*, p. 83.

Its ability to develop chlorophyll in times of need suggests two hypotheses: that it has only recently abandoned the independent habits still followed by the other members of the family Convolvulaceæ, and that it has done so in much the same way as the mistletoes, though the latter have progressed by no means so far toward permanent parasitism.

It is hardly necessary to discuss whether the host is benefited by the encircling dodder, for the dodder is an annual, dying soon after ripening its fruits, into which it removes the greater part of the nutrient substances contained in and composing its body. Thus it leaves little or nothing for its host to absorb and feed upon. When it attacks shrubby perennials—*e. g.* willows—its effects are only impoverishing and debilitating; when it successfully attacks annuals, it exhausts and kills them. European growers of flax and clover find the dodder one of the most destructive enemies of their crops. The dodder is, then, a permanent parasite, the parasitism of which is complete, however, only when the host can supply it with all needed foods.

The most intimate associations between parasite and host, and the most complete dependence of a parasite upon its host, are found among the fungi and bacteria parasitic upon higher organisms. In these associations the parasite not only sends root-like absorbing organs into the host, but in many cases it is very completely enclosed within the host.* The parasitic fungi and bacteria, always wholly devoid of chlorophyll, are entirely dependent upon their hosts for both kinds of food, non-nitrogenous and nitrogenous. These foods they work over, assimilate, incorporate and consume, in their own ways, but the elaborated foods they must have. These, then, are examples of permanent and complete parasitism. About the nature of the association between green plants and the fungi which cause disease in them,—*e. g.* grape-mildew, potato-rot, wheat-rust, etc.—there cannot be the least question: the host gains nothing from association with the fungus, the parasite gains everything from association with the green plant.

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* This last is not without parallel among phanerogamic parasites, for *Rafflesia*, *Brugmansia*, and our own *Arceuthobium* (*Razoumowskia*) are more or less completely imbedded in the tissues of the host.

Only about those remarkable structures called lichens is there any difference of opinion. Lichens are composed of algæ and fungi living together. The algæ—green, blue-green, or brownish—contain chlorophyll, and by its aid manufacture non-nitrogenous foods from carbon-dioxide and water. Nitrates they absorb in solution. From these and the sugars they elaborate amides and proteids like other independent plants. The fungi, on the contrary, devoid of chlorophyll, cannot elaborate non-nitrogenous foods and must absorb them ready formed. In the lichen the fungus is always closely applied to the algal cells, sends out short branches which clasp the algal cells, and, in a considerable number of already reported cases, these short branches send still shorter haustoria into the algal cells.* Whether only closely applied to the walls, or sending haustoria into the cells, the fungus filaments are so placed that they can draw food by osmosis from the alga. Because of the small size of the alga, the always larger fungus cannot become entirely enclosed within it; on the contrary, the fungus surrounds the alga with a more or less firm mycelium, confining the alga between the parts of its body. The association of fungus and alga, always intimate enough for the fungus to supply itself osmotically with non-nitrogenous foods elaborated by the alga, is in many cases so exhausting to the alga that many of its cells become entirely emptied. In spite of this evidence of the complete parasitism of the fungus, some botanists claim that the alga benefits also. It is alleged that the carbon-dioxide exhaled by the fungus, the mineral salts dissolved and held in solution, the protection against too rapid drying, too intense illumination, and too sudden changes of temperature, are of sufficient value to the alga to compensate it for the food taken from it and for the deformities and limitations in its growth. It may be true that all these benefits do accrue to the alga—though this is very far from being demonstrated—but even if this be true, are these benefits needed, are they not superfluous? Man's association with his domesticated animals is beneficial to them, but are these animals really any better off than by themselves in nature? Even if man's association with them is beneficial for the time, in the end it is fatal or, at least, onerous. The absolute dependence of the fungus component of the lichen upon some green plant for food, and the damage and death to the alga wrought by the fungus, furnish the strongest evidence that the association is not *equally* beneficial to the two members, mutually beneficial though it is sometimes claimed to be.

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* Peirce, G. J. The nature of the association of alga and fungus in lichens. Proc. Cal. Acad. Sci., Series III., Botany, vol. I., 1899. The relation of fungus and alga in lichens. American Naturalist, vol. XXXIV., 1900.

In these cases, we have examples of the stages through which parasitism has advanced—*first,* green plants, incompletely and only periodically parasitic; *second,* plants normally not green, permanently parasitic, and completely parasitic when the host is suitable; *third,* plants never green, permanently and completely parasitic.

The bacteria living in the bodies of animals, either intercellularly or intracellularly, absorbing already elaborated foods, utilizing these by processes fundamentally like those already discussed, present no new physiological principles, and hence those who would know more of this, as of the other special groups of organisms which we have just been discussing, must turn to the treatises devoted to them.

OTHER ELEMENTS ESSENTIAL TO PLANTS

The physiological chemistry of the other elements concerned in the nutrition of plants is still so vague that little can be said about them till further investigations give definite facts to deal with. These elements are obtained in analyses of plants in the form of incombustible compounds forming the ash resulting from combustion. For this reason they are collectively termed *ash-constituents,* to distinguish them from hydrogen, oxygen, carbon, and nitrogen, which go off in drying and burning. Besides the salts containing the elements absolutely essential to the normal nutrition of the plant, others are invariably present in the ash because they are present in soluble form in the soil. Though some few of these may be useful, they are not necessarily essential.

Chemical analysis reveals whatever is present in the plant-body, but neither indicates the compound in which an element exists in the living body, nor enables one to distinguish between necessary substances and those present in the plant simply because they are present in the media in which it lives—in soil, air, and water. Only by the culture of plants in media of known composition can the essential elements and compounds be distinguished from the non-essential, the useful but not essential from the absolutely useless and the absolutely necessary. Analysis shows that ordinarily 1.5-5% of the dry weight of plants is furnished by the ash constituents of all sorts, though in some cases 10-30% is ash. Analysis alone cannot account for this discrepancy. Culture in media of known composition shows that the greater amount of ash is due to peculiarities of the soil or to peculiarities of certain species or even families of plants. For example, 18-23% of the ash of Indian Corn is silicic dioxide, useful to the plant in hardening its outer surfaces and making projecting parts and the edges of leaves harsh and cutting, but not essential to its stiffness, growth, and perfect maturity.* Diatoms and the scouring-rushes (*Equisetum*) are much richer in silica than the grasses, but it is not yet proved that it is indispensable even for them.

Analysis reveals the presence of sodium and chlorine, as common salt, in all plants. Because culture without these elements is so difficult that it is doubtful whether it has ever been accomplished, no one can say whether they are absolutely essential or not. Experiment has already conclusively shown, however, that they are needed only in the smallest possible quantities if at all, though in certain cases larger quantities may act as favorable stimulants. This last is especially evident in the bacteria, the growth of which in the artificial culture media and under the unnatural conditions of the laboratory seems to be facilitated by the addition of a small amount of common salt to the culture. The ash of strand and marine plants contains a larger percentage of sodic chloride than that of inland plants. This is due simply to the presence of so much salt where they grow. Strand plants do not need salt, as is proved by cultures.* Inland plants are unfavorably influenced by a percentage of salt, in the soil or in water, which strand plants bear without injury. These last have succeeded in becoming adapted to conditions which preclude or minimize competition from more sensitive forms. The adaptations are discussed in the rapidly increasing literature on the ecology of the so-called halophytes.† Although the common salt in sea water is needed as food only in the smallest quantities if at all by the marine algæ, they will bear only the most gradual transfer to fresh water. This is probably due, however, to the greater density of the sea water, and this depends upon the other salts dissolved in it as well as upon this single one.

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* Quoted by Pfeffer (Pflanzenphysiologie, Bd. I., p. 429, Engl. transl. p. 435) from Sachs (Flora, p. 52, 1862).

An interesting experimental study of strand and other plants with relation to common salt and sea water has recently been made by Coupin.‡ He finds that 1.5% of common salt in soil or in water is poisonous to plants which do not naturally grow on the sea-shore. Since sea water contains about 2.5% of common salt and the soils bathed by the sea contain still more than this proportion, we can readily understand the sharp line which separates the marine and strand floras from those of the interior. Coupin attributes the poisonous property of sea water for inland plants mainly to its content of common salt, for the two salts next to this in abundance, magnesium sulphate and chloride, are present in quantities which he says are below the toxic proportions. Magnesic sulphate is poisonous at a concentration of 1%, magnesic chloride at 0.8%, but they occur in sea water only to the extent of 0.75% and 0.6% respectively. For strand plants the proportions of common salt are very different, as these figures indicate:

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* See Nobbe in Versuchsstationen, Bd. 13, 1870, the literature there cited, and Pfeffer, Pflanzenphysiologie, I., p. 424, etc., Engl. transl. I. pp. 429, 30, etc.

† For example, Schimper, A. F. W. Pflanzengeographie auf physiologischer Grundlage, Jena, 1898.

‡ Coupin, H. Sur la toxicité du chlorure de sodium et de l'eau de mer à l'égard des végétaux. Rev. génér. de Botanique, T. X., 1898.

	Fatal.	Injurious.	Harmless.
Beta maritima	4%	3%	2.6%
Atriplex hastata var. maritima	5%	4%	3.5%
Cakile maritima	4%	3%	2.8%

For these three plants 3% of magnesic sulphate, 2.5% of magnesic chloride, are poisonous. From these figures it is obvious that strand plants are very accurately adapted to the amount of common salt to which they are exposed, and that they can withstand much more of the other salts than they are ever exposed to.*

The soluble compounds of zinc are poisonous to all plants. In quantities not excessive when first encountered, or in amounts to which the special plants have become accustomed by long habit, zinc salts seem either to be ineffective or else to act as stimulants to more active growth and life.† It is claimed that there is a flora characteristic of soils rich in zinc. This is an exaggeration, but it cannot be denied that certain plants are found on zinc soils and not elsewhere (*e. g. Viola calaminaria* and *Thlaspi calaminarium*). These, however, are varieties of other species (*viz.* of *V. lutea* and *T. alpestre*), the variation being induced by the poison.‡

Aluminum salts, though of very general occurrence, are found in quantity only in the lycopods.[*] It is doubtful whether aluminum is necessary or even useful for these plants.

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* Schimper claims (*L. c.* pp. 98–102) that plants living in soils rich in freely soluble salts like sodic chloride, saltpeter, etc., present structural and other characters almost identical with those of desert plants. This he regards as evidence that halophytes as well as xerophytes seek to reduce transpiration, the latter because of the scarcity of water, the former because of the presence in it of poisonous compounds.

† Richards, H. M. Beeinflussung des Wachsthums einiger Pilze durch chemische Reize. Jahrb. f. w. Bot., Bd. 30, 1897.

‡ Schimper, A. F. W. Pflanzengeographie auf physiologischer Grundlage, Jena, 1898.

The essential soil (ash) constituents, as shown by water-culture, are salts of phosphorus, sulphur, potassium, calcium, magnesium, and iron. Calcium seems to be unnecessary for fungi, though indispensable for higher plants.

Phosphorus is a constituent element of protoplasmic matters. In the nucleins it may amount to 6%. According to Wolff's analyses,[†] phosphoric oxide (P_2O_5) constitutes about one-third of the ash obtained from embryonic tissue. This tissue is rich in protoplasmic matters. In older tissues containing a smaller proportion of protoplasmic matters, and in dead and emptied cells, the amount of phosphorus compounds is much less. In the total dry weight of a plant, the amount of phosphorus, calculated as phosphoric acid, is slight. This is shown by the following figures—[‡]

in lupine seeds	1.63%
" " straw	0.30%
" potato tubers	0.63%
" wood of trees	0.05%

Though the percentage of phosphorus in the body of an organism indicates the degree to which it is used, it by no means indicates the degree in which it is needed. Without phosphorus, protoplasm could not exist.

The source of phosphorus for the majority of plants is the phosphates in soil and water. Other plants under natural conditions may at all times supply themselves with phosphorus from its organic compounds in humus, in dead bodies of plants and animals, and in living bodies. The phosphates are less freely soluble in water than the salts of the other necessary elements; but since plants demand only small quantities, and since the carbon-dioxide and possibly also other acid secretions of their roots dissolve them more rapidly than does pure water, plants secure under ordinary conditions in nature all the phosphates needed. Manuring with phosphates has to be resorted to only when the soil has become impoverished by the removal of the crops cultivated upon it.

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[*] Pfeffer, W. Pflanzenphysiologie, I., p. 432, Engl. transl. I., p. 437. *L. Chamæcyparissus* and *L. Alpinum* have 22-27% aluminum in the ash, while *L. phlegmaria*, *Selaginella*, etc., contain only traces. Yoshida, H. On aluminum in the ash of flowering plants. Journ. Coll. Science, Imperial University, Tokio, 1887. In analyses of rice, wheat, oats, beans, etc. the Al. varies from 0.05% to 0.27% of the ash.

[†] Quoted from Versuchsstationen, Bd. 30, by Pfeffer in his Pflanzenphysiologie, I., p. 407, Eng. transl. I., p. 414.

[‡] Frank, A. B. Lehrbuch der Botanik, Bd. I., p. 587. Also in reports of State Agricultural Experiment Stations, etc., similar figures may be found.

In the plant phosphorus occurs not only as a constituent element of living protoplasm, but also in those already highly elaborated substances to be used in the construction of protoplasm, and in the simpler compounds formed by the breaking up of living or lifeless protoplasmic matter. The compounds of phosphorus occur, therefore, in the plant as solids—as parts of its structure and as stored material; also in solution—as constructive material and as the products of destructive metabolism.

SULPHUR, also a constituent element of protoplasm and therefore always present in the ash of plants, is found in even smaller proportions in the plant-body than phosphorus, as the following figures show—*

in lupine seeds	0.36%
" potato leaves	0.43%
" " tubers	0.24%
" wood of trees	0.025%

The source of sulphur for most plants is the various salts of sulphuric acid commonly found in the soil and dissolved in ordinary waters. Dependent plants—the so-called parasites and saprophytes—may perhaps obtain some sulphur in the form of organic compounds. The moulds can use salts of sulphurous acid, if present in sufficiently dilute solution,† although they are nearly as poisonous to all higher plants as sulphurous oxide and dioxide, gases poured forth in considerable quantities from chimneys in which inferior sorts of coal are burned.* .A few species of bacteria use as food-material, as well as their source of energy by respiration (see page 20), the sulphuretted hydrogen and metallic sulphur occurring in considerable quantities in mineral springs and set free in decompositions taking place in the ooze under bodies of water.

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* **Frank, A. B. Lehrbuch, I., p. 586.**

† **Quoted by Pfeffer from Nägeli, Bot. Mittheilungen, Bd. 3, 1881.**

Sulphur occurs in plants in the elementary condition only in well-fed sulphur bacteria. In these, as in all other plants, it occurs also as a constituent of protoplasm. A few plants, notably the *Cruciferæ*, contain sulphur in mustard oil, and it is a constituent of the garlic oil in the various species of *Allium*.

Nothing whatever is known of the stages through which the amides are elaborated into protoplasmic matters by the addition of sulphur and phosphorus.

POTASSIUM, although not a constituent element of protoplasmic substances, is an indispensable food-constituent. The compounds of sodium, frequently much more abundant, fail to serve as complete substitutes, although in the presence of an abundance of sodium salts plants demand less potassium than otherwise. In the total dry weight of plants potassium occurs in much larger amount than sulphur and phosphorus—†

in potato tubers	2.27%
" " plants	2.53%
" tobacco leaves	4.99%
" young red clover plants	3.59%
" lupine seeds	1.31%
" wood of trees	0.05%-0.15%

Potassium salts are most abundant in young and growing parts, least abundant in those which have ceased to grow or to be otherwise active, and from which the potassium has been withdrawn. From this it appears that potassium compounds are intimately concerned in the construction of protoplasmic matters. What compounds these are is not now known, though it is evident that potassium may be a component of reserve foods. Nobbe's hypothesis* that potassium salts are directly concerned in the translocation of the starch formed in chlorophyll-containing cells is interesting, because it suggests one of their possible uses in the plant, but that this is their main function follows neither from his experiments nor his arguments.

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* The striking absence from certain cities in which one might otherwise expect to find them, of lichens and other plants especially sensitive to gaseous poisons, may be attributed to the poor coal.

† Frank. Lehrbuch, I., p. 589.

According to Copeland,† the potassium salts are "an important part of the osmotically active material which keeps the cell and plant turgid," and "there is no experimental ground for attaching this significance to any other constituent of the mineral food."

Potassium salts are never very abundant in soils. They occur as sulphate, phosphate, and chloride, freely soluble, and hence easily washed away as well as absorbed. It is necessary frequently to manure soils with potassium salts when tobacco and other crops demanding considerable amounts of potassium are cultivated year after year on the same soil.

CALCIUM is neither a constituent of protoplasm nor necessary to all plants. For the fungi, and perhaps for certain algæ,‡ it is entirely unnecessary, magnesium successfully taking the place of calcium, besides performing its own part in nutrition. All other plants demand both calcium and magnesium. Unlike the elements already considered, the salts of calcium are found in tissues which have attained their full growth and in which work of another kind is especially going on, namely, in the chlorophyll-containing food-making cells of the leaves and cortex. In organs in which elaborated foods are stored, and in such dead parts as the wood, calcium salts are less abundant. These facts are indicated by the following table—*

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* Nobbe, in Landwirtschaftliche Versuchsstationen, Bd. 13, 1870.

† Copeland, E. B. Relation of nutrient salts to turgor. Botanical Gazette, Vol. 24, 1897.

‡ Molisch, H. In Botanisches Centralblatt, Bd. 60, 1894, and Sitzungsber. d. Wiener Akademie, Bd. 103, 104, 105, Abth. I., 1894, 1895, 1896. Benecke, W., in Botanisches Centralblatt, Bd. 60, 1894. Jahrbuch f. wiss. Botanik, Bd. 28, 189, and Botanische Zeitung, 1896.

Potato leaves have	2.90%	of dry weight as calcium salt.
" tubers	0.10%	
Pea straw	1.88%	
" seeds	0.13%	
Tobacco leaves	6.18%	
Hop "	7.38%	
Wood of trees	0.02–0.10%	

From such figures, the result of gross analyses confirmed by microchemical tests, it has been inferred that calcium is concerned in the formation of cell-wall and in neutralizing the oxalic acid set free in various chemical changes (notably respiration) taking place in plant cells. Proof that these inferences are correct is still lacking, however.

Loew's hypothesis† that the framework of nucleus and plastids is a double organic salt of calcium and magnesium, or a complex union of calcium and magnesium compounds, is a hypothesis only, and hence need only be mentioned.

The value of calcium to higher plants is beyond question, but how it is used is still unknown. It is found in plants usually as the oxalate (crystallized out as needles or as polyhedra of more symmetrical dimensions), as carbonate (deposited in the peculiar outgrowths of cell-wall known as cystoliths), much less frequently as sulphate and phosphate. Calcium salts are abundant enough in the soil to be taken up by all plants, and although the sulphate and phosphate are only slightly soluble, the large volumes of water absorbed will still carry adequate amounts, even from soils which contain little or no other calcium compounds, to the cells using them.

MAGNESIUM, absolutely indispensable to all plants,‡ in spite of the assertions of earlier authors to the contrary,§

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* Frank's Lehrbuch, I., p. 590.

† Loew, O. Über die physiologischen Functionen der Calcium-und Magnesiumsalze im Pflanzenorganismus. Flora, 1892. Über das Mineralstoffbedür f. niss von Pflanzenzellen. Bot. Centralblatt, Bd. 63, 1895.

‡ Molisch, H. *L. c.* under calcium. Benecke, W. *L. c.* under calcium.

§ Nägeli. Botanische Mittheilungen, Bd. 3, 1881 and others.

is even less understood in its physiological relations than calcium. As phosphate it may stand in some relation to the formation of protoplasmic matters, although it is not a constituent element of protoplasm. Like calcium, it occurs as a constituent of some of the reserve foods stored in such oily seeds as Castor Bean (*Ricinus*) and Brazil Nut (*Bertholetia*); but even here, in these complex compounds, it is not clear whether it is the magnesium (or calcium) itself, or the acid radicle of the salt, which is valuable.

IRON. Although this element is not known to be a constituent of protoplasm or of any compound incorporated into the living protoplasm, it is indispensable to all plants. The minimum needed is, however, smaller than that of any other element. If more than the minimum amount of iron is supplied, growth seems to be proportionally stimulated.* Unless green plants receive enough iron they will not be able to form chlorophyll, although iron is not a constituent element of any chlorophyll pigment. Plants remaining white from lack of iron are said to be chlorotic. Chlorosis may be regarded either as the evidence of an abnormal state of health or as the disease itself. The former seems by far the more probable.

The plant ordinarily obtains all the iron it needs from the salts of iron dissolved in all natural waters. Sometimes, however, chlorosis occurs in spite of the abundance of iron in the soil. When a shoot grows so rapidly that iron salts do not reach the developing parts rapidly enough, the new leaves will be white instead of green.

Some of each of the necessary elements found in the ash of plants is necessary to the normal development of the plant. The plant will develop normally only when it can obtain an amount of mineral matter in solution more than equal to the sum of the minimal amounts of each of the ash constituents. In virgin soil, and in the natural forest, the soil waters will contain all the necessary mineral salts dissolved in sufficient quantities for normal growth. Where man interferes by defective cultivation or mistaken selection of crops, the soil must be artificially enriched. In nature the constant supply of adequate amounts of all the food-materials is secured by the action of those forces and organisms which break down the inorganic and organic matters on and in the upper layers of rock and soil.

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* Richards, H. M. Die Beeinflussung des Wachsthums einiger Pilze durch chemische Reize. Jahrb. f. wiss. Botanik, Bd. 30, 1897. The effect of chemical irritation on the economic coefficient of sugar. Bull. Torrey Bot. Club, vol. 26, 1899.

CHAPTER IV

ABSORPTION AND MOVEMENT OF WATER FOOD DISTRIBUTION

In the preceding chapter we have discussed the elements and their compounds, which constitute the food-materials of plants, and we have gained some idea as to when, by what means, and through what stages these are elaborated into foods. How foods are assimilated—rendered like the living protoplasm which they are to nourish—is not now evident. We have finally seen that these assimilated foods may be incorporated into and made a part of the living protoplasm, but how this is accomplished remains one of the wholly unsolved problems of physiology.

We must now consider how the plant absorbs its food-materials and transfers from part to part the foods which it elaborates from them. These processes underlie and at the same time form an essential part of nutrition, but since other substances than those needed and used as food-materials and foods are concerned, we may well consider this subject by itself.

With the exception of water, which is both a food-material and the vehicle of nutrient substances, the food-materials of animals and plants are of two sorts—either gases or solids. The latter are available only in solution, entering the body and passing from part to part only when dissolved in water.* The absorption and transfer from part to part in the plant-body of the gaseous food-materials—carbon-dioxide, oxygen, and free nitrogen (when the last is used at all) —take place in accordance with the simple and generally known laws governing the diffusion of gases. We must, however, bear distinctly in mind that these gases are in two states in the bodies of all higher and of many lower plants. Through the stomata gases pass in the gaseous condition into or from the intercellular spaces, the air passages, etc. This movement through the stomata and in the intercellular spaces is strictly by diffusion, except where affected by mechanical forces such as compress or expand the air-spaces, etc., etc. But when gases pass through the cell-wall, into or out from a cell, their molecules mix with the water-molecules in cell-wall, protoplasm, and vacuoles, becoming dissolved in the water which the living body contains as an essential part of its structure. The movements of gases into and out from living cells, and from cell to cell, are therefore the movements of solutes (dissolved substances). The absorption of solutions into living cells, and their transfer from cell to cell, take place in accordance with the laws governing the diffusion of liquids. We can, therefore, study the movements of solids and of gases at the same time, for, so far as living cells are concerned, these two classes of substances behave alike. So far as the supply of solids and of gases to the living cells is concerned, we have to deal with different phenomena, and these we must study separately.

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* The apparent contradiction to this statement offered by the *Myxomycetes*, *Amœba*, etc.—naked masses of protoplasm not enclosed by cell-wall—which may in their movements surround solid particles, both innutritious and nutritious, is not a real one. Only those particles which are soluble and dissolved are *absorbed* by the protoplasm and really enter it; the others are left unaffected by it although they may remain *enclosed* for a time.

The water in the soil, and consequently all flowing water and that in pools, ponds, lakes, and in the sea, is a dilute solution of nutrient and other soluble substances from the air, from the mineral matters of the soil, and from the mixture of organic and inorganic matters collectively termed *humus*, which is found in all but the most sterile soil. The water of streams, ponds, lakes, and of the sea, is in the hydrostatic or massive state. After heavy rain, flood, or the melting of snow and ice, water is in the hydrostatic state in the soil also. Water in this condition can be drained off, but much will remain in other conditions, the amount depending upon the character of the soil. Soil which has been thoroughly drained, but not dried, will feel damp to the touch because of the considerable amount of water held in the capillary state between the soil particles. This can be removed by applying material possessing stronger capillary attraction, for instance, blotting or filter paper, which will quickly become damp by withdrawing water from the soil capillaries.* After soil has been dried as thoroughly as possible by removing the capillary water through stronger capillary attraction, water will still be retained in the hygroscopic state, held on the surfaces of the soil particles themselves. To overcome the attraction of the soil particles and to remove the last traces of water much greater force must be employed. In order to make soil absolutely dry it must be taken away from its natural position and exposed to some powerful dehydrating influence, *e. g.* concentrated sulphuric or glacial phosphoric acid in a desiccator, or, more simply, to heat in an open vessel. Another means of demonstrating the very considerable force by which soil particles attract and hold water and the substances in solution in it, is by filtering a dilute solution of some convenient copper salt or of Fuchsin through soil. The last trace of copper or of color will be removed from the solution, and the filtrate may be successfully used for the culture of plants, though the original copper solution would have been poisonous.

The amounts of water occurring in the hydrostatic, capillary, and hygroscopic states in soils will vary with their composition, with the fineness of the particles, and with their compactness on the surface.† It is essential that plants growing in coarse soils which drain rapidly, and in regions where no rain falls during the growing season, should be able to supply themselves with water even after the hydrostatic and capillary waters have been entirely removed from those layers of the soil traversed by the roots. To accomplish this it is absolutely necessary that the plant should be able to exert sufficient force to draw into its own body the water so strongly held on the surfaces of the soil particles. In California, the only water upon which most plants not subjected to irrigation can draw during the greater part of the dry season is that held hygroscopically, and that plants grow at all or even survive during the dry season is positive evidence that they do exert such an attractive force. What are the means at hand? To answer this question we must consider the physical properties of vegetable cells.

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* It must, of course, be noted that the cellulose walls of the capillaries in filter paper also imbibe water.

† See Year Book U. S. Dep't Agriculture, 1897, p. 129, report by M. Whitney, and also other papers on Soils published by U. S. Dep't Agriculture.

The typical vegetable cell—an alga, a root-hair, a parenchyma cell—is bounded by a thin cellulose membrane permeated with water holding in solution a variety of mineral and other substances. This membrane is firm, strong, elastic, and is not only permeated with water, *i. e.* has molecules of water between its molecules or groups of molecules, but also permits the movement of molecules of water and of substances in solution in water in and through itself. The movement of water and of aqueous solutions through a membrane is known as osmosis. Lining the cellulose wall is the layer of living protoplasm which produced it. The layer of protoplasm not only varies in thickness, being thickest in young and thinnest in old cells, but is never homogeneous. Apart from the nucleus, chromatophores, and granules of food and other substances contained in it, the surface of the protoplasmic layer in contact with the cell-wall is differentiated into an exceedingly thin living membrane, the ectoplast. Within the living protoplasm are the vacuoles—one or more bodies of water holding in solution a great variety of compounds, organic and inorganic —and the nucleus, also bounded, like the living protoplasm against the cell-wall, by cytoplasmic membranes. The membranes bounding the vacuoles are called tonoplasts. The solution filling the vacuoles and permeating the cell, the cell-sap, is the active agent in absorption, although its composition, and therefore its action, are controlled by the living protoplasm, either by the substances formed by the protoplasm and transferred to the cell-sap, or by the substances permitted by the cytoplasmic membranes to enter or pass out of the cell, the vacuoles, or the nucleus. That the cytoplasmic membranes do exert a controlling power over substances in solution in the vacuoles and outside the cell is evident from the following. Under normal conditions the protoplasm is slightly alkaline, the cell-sap slightly acid. If the cytoplasmic membrane bounding a vacuole (the *Vacuolenhaut*, as Pfeffer calls it) were permeable to all substances, and equally permeable in both directions, this difference in chemical reaction could exist only momentarily; it could not be the normal condition. Furthermore, so long as the cells are alive, no color will pass from clean slices of beet or of red or black cherry, or from other tissues composed of cells containing colored sap in the vacuoles; but if the cells are killed by immersion in hot water or by steam, the color will rapidly pass out into the water. Again, although harmless coloring solutions will pass into and stain the walls, the majority of such solutions, no matter what their concentration, will not pass into the protoplasm or stain any part of it, so long as the cells are alive. Some few harmless stains, if applied in sufficiently dilute solutions, may be employed to stain living protoplasm* and nuclei,† or may be accumulated in the vacuoles‡ of living cells.

From these experiments it is obvious that the living protoplasm, especially the structurally and physiologically differentiated layers adjoining the cell-wall and bounding the vacuoles and nucleus, do exercise some control over the dissolved substances adjacent. That this power is limited is shown by the above experiments with staining agents, by daily experience in the laboratory with the various poisons employed as fixing agents for histological purposes, and by the sensitiveness of plants to the soluble substances by which they are surrounded. If the cytoplasmic membranes could exclude poisons, at the same time allowing nutritious solutions to enter freely, the advantage would be great.§

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* Pfeffer, W. Über Aufnahme von Anilinfarben in lebende Zellen. Untersuchungen aus d. bot. Institut zu Tubingen, Bd. II.

† Campbell, D. H. The staining of living nuclei. Ibid.

‡ Pfeffer, W. *L. c.*

§ The living cell may, however, control the osmotic exchanges taking place between itself and the solutions outside, not only by regulating the composition of the cell-sap, but also by changing the permeability of the cell-wall. See Nathansohn, Zur Lehre vom Stoffaustausch. Ber. d. D. Bot. Gesellsch., XIX., pp. 509–13, 1901.

The living plant-cell is then a series of concentric permeable (or partially permeable) membranes of different composition, properties, and needs, surrounding and enclosing one or more bodies of water holding various substances in solution. Under ordinary conditions the density of this aqueous solution is greater than that of the solutions outside the cell, and its composition is different. The difference in density is maintained in land plants, as we shall see from another section of this chapter, by the loss of water from the leaves; the difference in composition is due to the activities of the protoplasm. In constantly submerged aquatics the means of maintaining the density of the cell-sap is less obvious, for from these plants no water is lost by evaporation, and no concentration by this means takes place. Although the water in the cells of algæ may not be lost or changed, the same result as regards the density of the cell-sap may be attained in another way. If one or more soluble substances are formed by the protoplasm and transferred to the cell-sap faster than they can pass out into the surrounding water, greater density will be maintained. It is upon the density and composition of the cell-sap, whether this is accumulated in larger volumes in vacuoles or is uniformly distributed throughout the living protoplasm, that absorption depends.

DIFFUSION AND OSMOSIS

Let us turn aside for a moment from the living cell to consider some of the purely physical phenomena and principles underlying the physiological process we are studying. If two equal volumes of liquid of exactly the same composition—say, two volumes of pure water—are brought into contact with each other, there will be molecular movements in and between them, but there can be no change in the composition or pressure or any other quality of either. Suppose five grammes of common salt to have been perfectly and uniformly dissolved in one of these volumes of water before the two were brought into contact. As a result of bringing the two volumes of water into contact the molecular movements in and between the two volumes will produce a change in the composition of both. The molecules of salt, being free to move not only through the one volume in which they were dissolved, but also into and through the second volume, will do so, and there will therefore come to be finally an equal distribution of salt molecules in the two volumes, each volume then containing two and one half grammes of salt. To such molecular movement, unaided by stirring, jarring, or other mechanical means, the name diffusion is given.* Let us suppose now that one volume of water contained five grammes of common salt and the other five grammes of any other salt, say potassium nitrate. The diffusion of the common salt from the first into the second volume of water, and of the potassium nitrate from the second into the first volume of water, would be at practically the same rate as into pure water. Theoretically there should be a difference in rate; actually there is no difference which can be detected. There would presently be two and one-half grammes of common salt and two and one-half grammes of potassium nitrate in each volume of water. But if we had five grammes of common salt in one volume and two grammes of the same salt in the other, the diffusion would not be so rapid, although the mixture would finally be as perfect. The rate of diffusion will vary with the difference in the proportions of salt in the two volumes, the greater the difference at the beginning the more rapid the diffusion; the nearer the proportions come to being equal the slower the diffusion, till, ultimately, with equal proportions, the diffusion ceases. So long as there is no chemical action of one salt upon another, this rule applies as well to solutions containing mixtures of salts as to solutions of single salts.

If now we bring together two equal volumes of pure water, only interposing a permeable membrane (bladder, vegetable parchment, cell-wall) between them, there will be the same molecular movements as in the first case above supposed, but there can be no change in composition. Similarly there will be movements of the salt as well as of the water molecules through the membrane if, in the other cases, we separate the two volumes of liquid by a permeable membrane. As we have already seen (p. 106), this form of movement, of diffusion, is called *osmosis*. The rate of osmotic transfer will vary for every salt according to the difference in the proportions of the salt in the two adjacent liquids. This difference is known as the *osmotic pressure*. Furthermore, the rate of movement will differ with the salt, with the composition, thickness, etc., of the membrane, and with other factors (*e. g.* the relations of the salts to one another, with the dissociation, etc.) which find their natural place for discussion in a text-book on physics.*

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* Illustrative experiments on diffusion are described in Darwin and Acton's and in the other laboratory manuals of plant physiology already referred to (p. 27).

Turning back now to our vegetable cell—an alga, a root-hair, a parenchyma cell, etc.—a body consisting of aqueous solutions enclosed in and permeating concentric membranes of different physical and chemical properties, we see that we have precisely the conditions imagined in our discussion of the purely physical phenomena. The cell-sap is a solution greater in density than the water outside the cell and differing from it in composition. In consequence, molecular movements will take place into and from the cell. These movements will tend to reduce the density and modify the composition of the cell-sap. Because of the greater density of the cell-sap—in other words, because of the smaller proportion of water in the cell-sap to substances dissolved in it—water molecules will pass into the cell through the cellulose wall, the cytoplasmic membranes, and the protoplasm, *diffusing* throughout the cell as well as in the vacuoles. Thus the density of the cell-sap will be lowered, the proportion of water to substances dissolved in it will be raised, and the volume of the cell-sap will be increased. But if the cellulose-wall resist any increase in the volume of the cell-sap and of the cell, the cell-sap will be subjected to pressure, the protoplasm will be forced by this means against the cell-wall, the cell-wall itself will be stretched, the whole cell will be in a state of tension, will be plump, will be *turges-*

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* See, for example, Ostwald's Solutions, translated by M. M. P. Muir, London, 1891.

cent. The pressure of the cell-sap and of the cell brought about by this means is called *turgor*, and it is evidently a very important factor in maintaining the form of the cell and, therefore, comprehensively, of the organs and of the individual. The turgor or turgescence of the cell tends to be maintained by the continued absorption of water; but unless the absorption continually exceed the loss of water, by evaporation or otherwise, there will be no turgor, the plant will be flabby, wilted. Absorption of water can be continued only by keeping the density of the cell-sap always greater than that of the water outside.

The production, control, and maintenance of this physical condition is accomplished in part by the living protoplasm, in part, in multicellular plants, by the osmotic absorption of water from one cell by another. In the latter case, water is drawn off by physical means only, and in obedience to unavoidable physical law, by the cells that need it. In the former case, the living protoplasm, by what it takes from and gives to the cell-sap in respiration, nutrition, and excretion, maintains the greater density of the cell-sap, that is, maintains the higher proportion of dissolved matter to water than prevails outside the cell.

Upon the *composition* of the cell-sap depends the absorption of the substances dissolved in the water outside the cell. We have already seen that a dissolved salt will pass through a permeable membrane into another volume of water which contains less or none of it, and that the rate of osmosis (or, in this case, of absorption) will depend upon the salt, the difference in the proportions of the salt in the two volumes of liquid, upon the nature of the membrane, etc. The cell—and by means of it, the plant—will absorb by osmosis those salts which occur in the soil and in water in proportions larger than in the plant. For example, common salt will be absorbed by a root-hair or by an algal cell until in the cell-sap there is the same proportion of salt to water as in the solution outside the cell. When there have come to be the same number of molecules of salt in equal volumes of cell-sap and outside water, there will be no further absorption of salt, and although the movements of salt molecules will continue, there will be no accumulation of these either within or without the cell. Common salt will be absorbed by the cell, therefore, as a purely physical necessity, regardless of the presence of the other salts dissolved in the cell-sap, and regardless of the fact that it is needed and used by the cell only in the minutest quantity if at all. On the other hand, if the common salt were used in quantity by the cell, or in any other way removed from the cell-sap (by decomposition, precipitation, or otherwise), the proportion of common salt to water in the cell-sap would always be lower than outside the cell, there would always be osmotic pressure inward, the molecules of salt would constantly force their way into the cell in the attempt to attain osmotic equality or balance, there would be continued absorption of common salt, and the rate of absorption would vary with the osmotic pressure. Such is the case with salts used by the cell or otherwise removed from their solution in the cell-sap. For example, the nitrates are, as we have seen, the best form in which nitrogen is taken in by most plants, and of these potassium nitrate is perhaps the most common. Potassium nitrate will be absorbed by the plant with an avidity proportioned to the need of nitrogen, or—to state this in physical instead of physiological terms—at a rate depending upon the difference in the proportions of potassium nitrate within and without the cell. If the nitrate be decomposed and the nitrogen used by the plant as fast as it is absorbed, the osmotic pressure will remain as great, the absorption will continue as rapid, as at the beginning. Upon the amounts needed, used, or otherwise taken out of the cell-sap by the living protoplasm will depend the amounts of different salts absorbed by plants beyond those amounts necessary to secure uniformity of composition in cell-sap and outside water if no salts were consumed. In this consists the so-called "selective power of roots" and of plant-parts in general.

We see, then, that the absorption by the cell of those substances which can pass through cell-wall, cytoplasmic membranes, and protoplasm is a physical necessity whenever there is any higher proportion of these substances outside the cell than in it. When there is no difference in proportion, there will be no absorption or no further absorption. When, by the vital needs and activities of the cell or of the plant, a difference is maintained, there will always be absorption, proportioned in rate to the difference, proportioned in amount to the duration of the difference. This accounts for the much higher percentage of potassium than of sodium in the ash of marine algæ. The amount of sodium salts absorbed is only such as to attain the osmotic balance of sodium salts in the cell-sap and in sea water, wherea the amount of potassium salts is such as to satisfy the need of the plant for potassium and for the elements associated with it in these salts. The accumulation of iodine in marine algæ is due, not to the demand of these plants for iodine, but rather for the element or elements with which the iodine is combined in sea water: the iodine is, therefore, removed from solution in cell-sap and accumulates in insoluble form in the cell.

THE MEANS OF ABSORBING NUTRIENT SOLUTIONS

From the foregoing discussion of the physical principles underlying the absorption of nutrient solutions, we can now understand how an alga supplies itself with adequate amounts of food-materials. A land plant, however, in addition to its demand for other food-materials, must regulate its absorption according to its demand for water to make good that lost by evaporation. We must now consider how the land plant adapts itself to the conditions prevailing on land and successfully employs the physical means of absorbing the nutrient salts in the soil.

The root is generally regarded as especially the absorbing organ of higher plants. The cells on the surface of the root, being the only ones which are directly in contact with the soil particles and with the soil water, are the only ones which can absorb solutions from the soil. Only the youngest of these cells have walls of such composition and thinness that osmosis can take place rapidly. Furthermore, owing to the granular nature of soils, and owing to the fact that the water, at times when it is most needed, is held longest and most strongly upon the soil particles, and not between them, no smooth cylindrical organ of the size of even the smallest roots will be able to bring enough of those cells capable of absorption into sufficiently intimate contact with a large enough number of soil particles to ensure the osmotic absorption of water from the soil particles into the root. For osmotic transfer, as we have seen before (p. 109), both of the two liquids concerned must be in contact with the permeable membrane. Furthermore, as is the case on soil particles, water strongly held as a thin film over an irregular surface will not rapidly move from part to part of that surface. To ensure the absorption of much water from such a surface, there must be the most extended proximity possible of the osmotically active liquids. The permeable membrane must therefore cover the irregular surface as widely and as closely as possible. The most intimate contact of absorbing cells and liquid to be absorbed will be effected when hairs of such size and length that they will fit the soil particles develop on the root.

The length, thickness, and number of root-hairs will vary according to the medium in which they develop, and also according to the amount of water given off by the plant. The root-hairs will be numerous directly in proportion to the difficulty of getting enough water. This can be easily demonstrated by cultivating young seedlings of corn with their roots in moist air, in soil, and in water. The root-hairs will be most numerous in the air, less in the soil, and there will be exceedingly few if any in the water. The length of the root-hairs will also differ strikingly; they will be longest in the air, shortest in the water. The diameter of the hairs is necessarily limited by the size of the epidermal cells of which they are branches, but within this limit the hairs certainly vary according to the size of the soil particles among and around which they must grow. That the root-hairs not only grow between the soil particles, but actually apply themselves very closely to them, is abundantly proved by the common experience of up-rooting plants grown in loose soils. When such plants are pulled up gently, numberless soil particles of minute size cling to the roots, held there by the root-hairs, just as larger lumps of soil are held by the root-branches.

The function of root-hairs is to absorb nutrient solutions from the soil. They, and their physiological equivalents, the rhizoids of lower plants, are the chief absorbing organs of larger plants. The roots themselves are for the conduction of the solutions absorbed by the root-hairs, and also for the mechanical support of the whole plant. The root-hairs should not be regarded merely as structures *increasing* the surface through which aqueous solutions are absorbed by roots; the root-hairs are the *main* surface through which the absorption takes place. But more than this, they are the very perfect means by which the only parts capable of copious absorption—living cells bounded by thin cellulose walls and containing cell-sap of proper composition and density—are brought into the necessary intimate contact with the nutrient solutions adhering to the irregular surfaces of the small soil particles. In other words, the root-hairs are the means of bringing together, so that they are separated only by a thin permeable membrane, two aqueous solutions of such osmotic pressures that the one enclosed will absorb the one held by surface attraction (p. 105).

It has been estimated* that the surface of a root is increased 5 to 12 times by the production of hairs. From what has just been said, and because the hairs are bounded by walls at least thinner if not otherwise more permeable than the cells between, we see that this does not necessarily fairly indicate the increase in absorbing power even of the part producing the hairs. This may be more than 5 to 12 times increased, according to circumstances.

The life of a root-hair is necessarily brief. Its delicacy, and the fact that it may be torn and broken by the continued forward growth of the part where it is borne, favor this. The root-hairs are formed by the outward branching of epidermal cells on that part of the root just behind the tip which has almost or quite ceased to grow in length. If any considerable growth in length does occur after the formation of the hairs, these must surely be dragged forward and broken. Secondary growth in thickness of the part will crush them. Each young and growing root or root branch is covered for a time by a zone of root-hairs. This zone will vary in breadth according to growth conditions. The hairs will vary in length, diameter, and number according to soil conditions. As the root grows, the work of the older and less effective root-hairs is taken up by the younger ones newly formed farther forward and nearer the growing point. In this way new soil-particles are relieved of their small stores of water, and the absorbing surface is correlated with the growth of the plant as well as with its demands in the stationary condition.

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* Schwarz, F. Die Wurzelhaare der Pflanzen. Untersuch. aus dem botan. Institut zu Tübingen, Bd. I., p. 140.

THE MEANS OF TRANSFER OF NUTRIENT SOLUTIONS

Similar to the differences between cell-sap and soil-water in density and in composition, which enable the root-hairs to absorb water and dissolved food-materials, are the differences in the density and composition of the cell-sap of adjacent cells. The cell with denser cell-sap will absorb water from its neighbor with more dilute cell-sap, the cell-sap with less of a needed food-material or food will absorb from one with more. Such osmotic transfers are inevitable wherever miscible solutions or liquids of different densities and compositions are on opposite sides of a permeable membrane and in contact with it. By osmosis the distribution of food-materials will take place through the body of a small land plant, *e. g.* a fungus or a liverwort, and in submersed aquatics. For all plants not subjected to the loss of water by evaporation, and in the bodies of most land plants so small and so simple as the liverworts and the fungi, the rate of transfer by osmosis alone is rapid enough to ensure the adequate distribution of water and of dissolved foods and food-materials. Larger land plants are subjected to such losses of water from their aerial parts that osmotic transfer is too slow always to keep pace with evaporation. In plants provided with special organs for excreting water (see pp. 126-8) these organs must be copiously supplied.

Evaporation and excretion, taking place on the exposed surfaces and also from those cells bordering on air-passages, increase the density of the cell-sap of the cells directly concerned. These draw osmotically upon their neighbors for water to make good their loss. The neighboring cells in their turn draw upon cells still more remote from the losing surface. In this way the demand for water is developed in cell after cell away from the surface. To meet the demand, water is transferred from cell to cell toward the surface. Ordinarily, cells are small and short, and though their bounding cellulose membranes and their component protoplasm may be freely permeable, water can move more rapidly in response to other than osmotic forces if only the way is clear. Through living cells water can make its way best by osmosis, but as water will pass more rapidly through a tube in which no filtering membrane is interposed, so water in the plant will pass more rapidly through elongated cells than through a series of short ones, through dead and empty tracheids than through living cells of the same dimensions (other things being equal), and through continuous ducts than through a succession of tracheids. These stages in the development of conducting tissues one finds in the larger erect mosses, in the Coniferæ, and in the Angiosperms. The most perfect development of a vascular system is found perhaps in twining plants, especially those of tropical countries,* in the slender stems of which the ducts are large, long, and no thicker walled than is consistent with the necessary mechanical strength.

Upon the vascular tissues, throughout their whole length, parenchyma cells abut directly. In the root these parenchyma cells receive more and more water so long as the root-hairs continue to absorb any from the soil, and presently, not being able to expand beyond a certain point by reason of the pressure of their neighbors, they are obliged to get rid of the excess in some way or other. Into the vascular tissues of the root, therefore, the parenchyma cells discharge the water and dissolved matters, the discharge taking place in the direction of least resistance, that is, from living and turgid cells into empty tube-like tracheids and ducts. At any point in the plant the adjacent parenchyma cells may absorb water from the vascular tissues just as the root-hairs absorb water from the soil, and by the same physical means. Whether there are continuous columns of water in the ducts or not, there is a continuous body of water in the walls of the ducts, and so the withdrawal of water at any point will induce a movement of water toward that point from parts better supplied. It is ordinarily from below that water is drawn, for ordinarily the root-hairs supply the needs of the whole plant, but this is not necessarily the case, for through the conducting tissues water will pass up or down according to circumstances.

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* Schenck, H. Beiträge zur Biologie der Lianen. Bot. Mittheilungen aus den Tropen, Bd. II., 1893.

The vascular tissues form a continuous system, often much complicated in arrangement but proportionally increased in usefulness, of water-conveying cells and vessels extending from base to tip of the plant. At frequent intervals the bundles, which run more or less distinct from one another, anastomose and thus combine the vascular tissues into one effective system. Branches are given off from the main channels, so that buds, leaves, branches, even hairs (*e. g.* glandular hairs of *Drosera*), are reached by the conducting system. By this means all the parenchyma cells, which are the actively living cells of the plant-body, are supplied directly or indirectly. The amount of water and of dissolved matters supplied to any part will depend upon the demand, upon the amount lost and consumed. For example, two adjacent vascular bundles, running to two leaves, will convey different volumes of solutions if from the one leaf more water evaporates than from the other, or if in one leaf more water and dissolved matters are used than in the other. We thus see that the amounts transferred through parts, and consequently through the whole, of the vascular system are dependent upon the activities of living cells: *first,* upon those living cells which absorb nutrient solutions from the soil and from which other living cells osmotically absorb them, the cells abutting upon ducts and tracheids discharging the excess of water into these empty spaces; *second,* upon the living cells of the aerial parts, in the leaves, branches, and stems, in which the solutions are worked over and from which the water is given off.

The living parenchyma cells near the absorbing cells in the roots, and the living parenchyma cells composing the food-making tissues in other parts may be many metres apart. The absorbing and consuming tissues of herbaceous plants are usually close together; in tall trees they are separated,* but are farthest from each other in some of the "lianes." How is the water raised from the low levels at which it enters the vascular bundles, in the region where it is absorbed from the soil, to the cells needing it but far removed?† This question has occupied botanists from the time when physiological experiments were first undertaken until now. Despite the most acute study, the question—one of the most alluring and important in botany—is still unanswered. Hypotheses, deserving respectful consideration both because of their reasonableness, and also because of the fame of their authors, have succeeded one another in the text-books, have been accepted and then discarded, according to the prevailing fashion. As Sachs was for many years the leading plant-physiologist, so his idea, laid down in his writings with all his brilliant power, that the water ascended only through the walls of the wood-elements,‡ was the only one echoed by the smaller text-books. Then followed § Godlew-

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* From Kerner and Oliver's Natural History of Plants these "certified estimates" of heights and lengths are quoted:—

Eucalyptus amygdalina—	140–152	metres—	page	722,	vol.	I.,	part	2.
Sequoia gigantea	79–142	"	"	"	"	"	"	"
Calamus Rotang	200	"	"	677,	"	"	"	"

In his Silva of North America, Vol. X., p. 141, Sargent makes the following statement regarding *Sequoia sempervirens:* "The Redwood, which is the tallest American tree, probably occasionally attains the height of four hundred feet or more. The tallest specimen I have measured was three hundred and forty (340) feet high."

† While this book is in the press, Copeland is publishing in the Botanical Gazette, vol. 34, 1902, "The rise of the transpiration: an historical and critical discussion."

‡ Sachs, J. von. The Physiology of Plants, Oxford, 1887, pp. 241-242.

§ Godlewski, E. von. Zur Theorie der Wasserbewegung in den Pflanzen. Jahrb. f. wiss. Bot., 1884.

ski's hypothesis, on the face of it much more reasonable, but not directly supported by experiment, that living cells adjoining ducts and tracheids exert a pumping action. By dissolving poisonous substances in the water to be absorbed by the plants selected for examination, Strasburger* attempted to demonstrate that living cells are not concerned. Sap-pressure (see pp. 127, 131) was for a time considered the propelling force, but the absence of sap-pressure at the times when water is most needed is sufficient evidence against this notion. The varying pressure of the gases within the body of the plant was supposed to be the answer to the question, until it was shown that gas-pressures do not vary enough and rapidly enough. Then came the era of Jamin's chains, when the ducts and tracheids, found to contain alternating columns of air and water, were supposed to furnish the tubes through which these pass. Schwendener,† Dixon and Joly,‡ and Askenasy § have contributed much to a knowledge of the physical qualities of such chains, but no one has succeeded in proving that they have much if anything to do with water-transfer. Repeatedly botanists have returned, from lack of anything better, to the idea that capillarity conveys the water through the vascular system; but this notion is inadequate because the vascular system of many plants is composed of tubes so small and so short that, although the capillary force is great, the resistances are also so great that a sufficiently rapid transfer by this means alone is inconceivable.

From all the contradictory views this much may be extracted as proved. The water, which certainly permeates the walls of the elements composing the vascular system, is also contained in the cavities and passes through the cavities in the direction of strongest attraction, conversely of least resistance. That the water does actually pass into and through the cavities of ducts and tracheids is demonstrated by using a solution of gelatine, which melts at a temperature so low as not to injure the plant, but which is solid at ordinary temperatures. For example, gelatine melted at about 30° C. will be taken into the freshly-cut butt of an amputated branch and can then be hardened by plunging into water at 20° C. If now the branch, with the butt freed from superfluous adherent gelatine, is stood up in a jar of cool water its leaves will wither. They will recover, however, if placed in water warm enough to melt out the gelatine. This experiment is significant in two ways at least. *First,* solid gelatine permeated with water is no bar to osmotic transfer of aqueous solutions, while paraffine, or any similar material which is impermeable to water but might also be used to fill the cavities of the vessels, would stop osmosis. We see then that osmotic transfer, even if it could take place in the ducts as it does between the parenchyma cells, is too slow for the conduction of more than small volumes of solutions and for short distances. *Second,* if the solidified gelatine is properly removed from the surface of the butt of the branch experimented upon, little or no penetration of gelatine into the walls of the ducts having taken place, the permeability and conducting-power of the walls will be only very slightly diminished if impaired at all.

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* Strasburger, E. Bau und Verrichtung der Leitungsbahnen, 1891. Über das Saftsteigen, 1893.

† Schwendener, S. In Sitzungsberichte der Berliner Akademie, from 1886 on.

‡ Dixon and Joly. On the ascent of sap. Annals of Botany, 1894. The Path of the transpiration current. *Ibid.*, 1895.

§ Askenasy. Über das Saftsteigen. Verhandlung d. naturh. Vereins in Heidelberg, 1895.

Further than this no positive assertions can be made. The water certainly ascends, mainly in the cavities of ducts and tracheids, though also in the walls, and whenever the physical conditions demand it, water and dissolved salts will be drawn from the phloem as well as from the xylem. The main path for the transfer of the solutions of food-materials is the wood; for the transfer of the solutions of elaborated foods, the phloem or bast-portion of the vascular bundles. The physical force needed to raise the water is still unknown.

Of the various views regarding the means of transfer to which reference was made on pages 119 and 120, one is further from disproof, perhaps also from proof, than the others. This is the one put forth by Godlewski,* and advocated in more or less modified form by a number of other authors. According to this view, the living cells which are always found to be the close neighbors of ducts and tracheids participate actively in raising water from roots to leaves. Apart from the anatomical relationship of these living and lifeless elements, which suggests that the living cells may aid in as well as influence the movement in the lifeless ducts and tracheids, it is definitely proved by experiment that it is the youngest wood, that is, the wood containing the most and the most active living cells, which transfers most water and does it most rapidly. The method of proof consists in using solutions of harmless coloring-matters not fixed by living cells (*e. g.* Indigo-carmin, Anilin Blue, etc.). If amputated branches are placed in such solutions the path of transfer will be indicated by the staining of cell-walls, and if the experiment is not prolonged, the stain will be found highest in the youngest, that is, the best-conducting wood. The "sap-wood" conducts most if not all of the water. On the other hand, the "heart-wood" conducts little or none. The heart-wood not only contains fewer living cells—the oldest heart-wood none at all—but its permeability diminishes as the infiltration of the walls with coloring, hardening, preserving, and other substances progresses. In the youngest wood, where there are the most living cells, the maximum transfer of water takes place.

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* **See Pfeffer, Pflanzenphysiologie, Bd. I., p. 208; Engl. transl., I., pp. 220** ***et seq.***

Against the idea that living cells are actively concerned in raising water from root to leaf are the conclusions drawn by Strasburger from his experiments. The following will serve as an illustration of one line along which he experimented.* A specimen of *Acer platanoides* twenty-one metres high was obliquely sawed through at the base, a strong stream of water playing constantly into the cut as the sawing progressed. The tree was then placed with the butt in water. After the lapse of a half-hour it was hoisted, the cut surface smoothed with a sharp knife, and then lowered into a 5% solution of copper sulphate. In two weeks it took up nearly 30 litres of this liquid and the presence of the copper could be demonstrated up to, but not in the finest and highest branchlets. The rapid ascent of so large a volume of poisonous liquid is alleged to prove that living cells are not necessary to the transfer. One very strong objection to this conclusion is this:—although any cell into which even a small amount of copper penetrates will be poisoned and killed thereby, the cell next above will not cease its activity until it in turn absorbs and is poisoned by the copper. Furthermore, it is well known that water, which already permeates all cell-walls, will ascend faster than substances dissolved in it but not permeating cell-walls. The poison will ascend less rapidly than its solvent because the copper-salt will be taken up by the cell-wall, and will diffuse osmotically through the cell. If then, living cells do take an active part in the transfer of water, the ones above and not killed by the copper can still pull up the solution though to their own ultimate undoing, and they will pull up water faster than copper salt.

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* **Strasburger, E. Bau und Verrichtung der Leitungsbahnen, p. 617, 1891.**

Whether living cells are actively concerned in water-transfer or not, the popular idea of the lifetime of a cell must be modified somewhat. Those trees which form no "heart-wood" and in which living cells may be found quite to the centre (*e. g.* Beech and Birch), and the Palms and other Monocotyledons which do not increase in thickness, offer striking examples of the age attained by living cells. Strasburger* reports finding living cells in large numbers almost to the centre in sections of seventy-year old beech trees.

In the wood of trees growing in regions with pronounced seasonal differences there are seasonal as well as age differences. The "annual rings" are divisible into so-called "spring-wood" and "autumn-wood," although the latter is formed long before autumn. The anatomical differences which distinguish these layers of the annual ring from one another are accompanied by differences in their conducting power. Spring-wood is formed at the time when sap-pressure is greatest, when the opening of buds is followed by the expansion of the leaf and other surfaces from which water can be given off, when the plant resumes all at once the activities which have been suspended for a season, and when most food as well as most water must be carried to the active parts. Spring-wood conducts better than autumn wood, although according to Strasburger,* single rows of cells formed last in the autumn-wood possess higher conducting powers than those formed earlier. This he regards as contributing to a better connection between the succeeding rings, and this is especially necessary because the new bundles for the forming and growing parts must be adequately supplied with liquid while the young spring-wood, with which they connect, is attaining effective dimensions. (For the cause of "annual ring" formation, see pages 191–4.)

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* *L. c.*, p. 534.

Perhaps in all plants, certainly in many plants growing in desert regions and in places where there is a distinct dry season, tissues are developed in which water may be stored and kept for a long time, in spite of the dryness of the surrounding air. It is quite possible that the wood-fibres, present always in the xylem of the vascular bundle and sometimes numerous there, serve as temporary holders of water at the same time that they contribute to the mechanical strength of the plant. After collenchyma has served its first purpose in strengthening the rapidly growing parts in which it differentiates so early, its thickened and chemically modified walls, as well as the living cells which formed them, retain water with considerable power.† The most striking examples of water-storing tissues are to be found among desert plants (*e. g.* in the Cactaceæ and Euphorbiaceæ),‡ and in the leaves of Sphagnaceæ, which live under exactly opposite conditions. The possession by swamp-plants, especially those living in undrained swamps and in bogs, of characters found otherwise only in desert-plants has been remarked by a number of authors. This may be due to the plants trying, by reducing evaporation and therefore the need of absorption, to avoid absorbing in excess any of the poisonous matters (humic acid, etc.) in swamps, or it may be due to the actual difficulty of absorbing water.*

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* *l. c.*, p. 592.

† Müller, C. Beitrag zur Kenntniss der Formen des Collenchyms. Berichte der Deutsch. Bot. Gesellschaft, 1890.

‡ See Goebel's Pflanzenbiologische Schilderungen *and* Volkens's Flora der ägyptisch-arabischen Wüste, 1887.

SECRETION

Before leaving the subject of the osmotic phenomena in the plant-body to discuss those of water vaporization and gas exchange, those osmotic processes which result in the removal of material from the plant should be mentioned. If there is absorption by means of osmotic currents set up and maintained because there are smaller proportions of water and of various other substances inside than outside the cell, there must be excretion by the same means whenever the opposite is true. Such excretion does take place; there are exosmotic as well as endosmotic currents. They are very different, however, in amount, rate, and character. By the root-hairs of higher plants water and dissolved substances are endosmotically absorbed. Minute quantities of a number of substances are exosmotically excreted also by the root-hairs. Since Sachs's classic experiment in growing roots in contact with polished marble plates,† it has been known that roots can exert a corrosive action on such solid matters as they touch. Recent experiments by Czapek ‡ have shown that the principal substances diffusing from roots are mainly carbon-dioxide (passing out as carbonic acid, H_2CO_3), phosphoric, hydrochloric, sulphuric, and phormic acids and their salts, preeminently substances which would aid the plant to obtain needed food-materials from the soil.

Besides the excretion from roots, the secretions in the various glands and reservoirs are dependent upon exosmotic movements. Nectaries are special organs on the surface of which sugar is abundantly produced. What causes the formation and excretion of sugar by the cells of nectaries is not known, but given the sugar on the surface of a nectary, the excretion of water to dissolve this is inevitable.* Why this sugary solution is not resorbed is also unknown. Apparently no clear idea of the action of nectaries can be had until the physiological chemistry of these organs is worked out.

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* Cowles, H. C. The ecological relations of the vegetation of the sand dunes of Lake Michigan. Botanical Gazette, vol. 27, 1899. Schimper, A. F. W. Pflanzengeographie auf phisiologischer Grundlage, 1898.

† Sachs, J. von. Auflösung des Marmors durch Mais-Wurzeln. Botanische Zeitung, 1860. Lectures on the Physiology of Plants, pp. 262, 263, Oxford, 1887.

‡ Czapek, F. Zur Lehre von den Wurzelausscheidungen. Jahrb. f. wiss. Botanik, Bd, 29, 1896. See also Sistini in Atti di Soc. Tosc. di nat., Proc. Verb., 1899 (reviewed in Just's Jahresbericht, Bd. 27, 2te Abth., p. 194), who says roots convert feldspar into clay, working at least four times as fast as the weather.

The accumulation of resins in the intercellular resin-reservoirs of the Coniferæ, etc., and the incrustations of lime and iron on the surfaces of various plants, are accounted for in the following way. Certain substances elaborated or formed as by-products by glandular cells, are excreted osmotically into intercellular spaces, or upon the surface, or under the cuticula (in certain hairs), there undergoing such chemical change that they are no longer capable of osmotic movement in water.†

The excretion of fluid water by many plants is also accomplished by purely physical means. Water vapor is universally given off by land plants (p. 136), but the escape of fluid water is a less frequent and regular occurrence. In nectaries the passage of fluid water from the cell is due to osmotic pressure, the attraction of the excreted sugar. In other cases, on the contrary, fluid water is excreted, not because of the attraction (osmotic suction) of substances outside the cell but because of the pressure (turgor, p. 110) within the cell.

Turgor will develop in a cell whenever the cell-sap, because it contains a higher percentage of dissolved salts than the water outside, can absorb water. The volume of the cell-sap and of the enclosing protoplasm tends to increase with the absorption of water. Such increase in volume is only feebly resisted by the mechanically weak protoplasm. It can be resisted only by the cell-wall, a strong, elastic, permeable membrane, composed of one of the celluloses. Turgor and sap-pressure result from the resistance by the cell-wall to increase in volume. If the sap-pressure in a cell becomes greater than the retaining power of the wall, something will change. The absorption of water may be stopped by modifying the composition of the cell-sap, by exosmosis of the osmotically active salts to other cells, or by chemical change of the salts in the sap; or water may pass out through the wall in a direction of less pressure, either into adjacent cells or out upon the surface of the organ. If none of these things occur and absorption continues, the cell-wall will break.

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* Wilson, W. The cause of the excretion of water on the surface of nectaries. Untersuchungen aus dem Bot. Institut zu Tübingen, Bd. I., 1881. Schimper, A. F. W. Wechselbezienhungen zwischen Pflanzen und Ameisen, 1888.

† See Pfeffer, Pflanzenphysiologie, Bd. I., pp. 115, 116 501; Engl. transl., pp. 129, 500. Kohl, F. G. Kalsalze und Kieselsäure in der Pflanze, 1889. Giesenhagen, C. Die radialen Stränge der Cystolithen von Ficus elastica. Berichte der Deutsch. Bot. Gesellsch., 1891. Tschirch, A. Die Harze und die Harzbehälter. Berlin, 1900.

The cortical parenchyma cells in the root, in the region where absorption through the hairs is taking place, are under sap-pressure—whence the misleading name of root-pressure—and consequently force water into the conducting elements, tracheids and ducts, with which they are in contact. The same process underlies the action of water-pores.

Certain weather conditions favor the excretion of water by making it possible to develop the necessary sap-pressure. When the air is warm and moist above a warm damp soil, there will be copious absorption through the roots and proportionally little loss of water from the upper parts of the plant by evaporation. Sap-pressure necessarily develops, and if these conditions continue, the pressure will presently exceed the retaining power of some or many cells, water will either filter through or break through the cell-walls. If it break through, a wound is formed, and the escape of liquid from it is bleeding (see pp. 130–36). Such wounds are not altogether uncommon.*

The filtering of water under pressure through cell-walls does not take place indiscriminately, for the permeability of the walls of the cells composing the different tissues is not equal. Thus, as a rule, the walls of superficial cells are so water-proofed, either by chemical change or by infiltration of the cellulose, that water will be pressed out of other cells before it will pass from them. The so-called water-pores—such as occur on the garden nasturtium—are merely the openings on the edges of the leaves of cavities at the tips of vascular bundles. The thin-walled cells bordering upon the ducts and tracheids of these bundles squeeze out water into them, the water makes its way toward the surface, escapes into the cavity, and finally passes out through the pore. The excretion of water can, however, be observed on many plants not provided with such highly developed filtering organs. On the leaves of grasses grown under glass in the laboratory, and on the filaments or erect fruiting bodies of various fungi similarly cultivated, water will collect in drops whenever the substratum is so moist that checking the evaporation will raise the sap-pressure to the filtering point. This occurs regularly in grass-plats at night. The "dew" there formed is mainly expressed water rather than moisture condensed from the air.

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* See Pfeffer, Pflanzenphysiologie, Bd. I., pp. 255 *et seq.;* Engl. transl., I., pp. 272 *et seq.* Strasburger, E. Bau und Verrichtung der Leitungsbahnen, 1891.

A considerable number of plants, especially those growing in damp tropical regions, rid themselves of superfluous water by means of living glandular hairs on the surface, usually the under surfaces of leaves. According to Haberland* these glandular hairs, to which he gives the name *hydathodes*, press out liquid only when living.

The liquid passing out of water-pores and excreted by hydathodes is usually a very dilute solution, mainly of mineral substances, with little or no sugar or other organic compounds. These organs are therefore quite different as to their products from nectaries.

Other water-excreting glands are not uncommon. The accumulation of water in the pitchers of *Nepenthes*, *Sarracenia*, *Darlingtonia*, the secretions on the hairs of *Drosera*, and on the leaves of *Dionea*, are due to the action of water-glands. The cells composing these glands change not only the rate but, as we have already seen (page 83), the kind of activity in accordance with certain stimuli. On the hairs of *Drosera,* and on the leaves of other carnivorous plants, the sugary secretion which is used for attracting and capturing prey may be more like that formed by nectaries (page 126)—due, so far as the water is concerned, to osmotic suction rather than to active pressing out. The filling up of the pitchers of the pitcher-plants is much more likely to result from active excretion of water.

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* Haberland, G. In Sitzungsberichte d. Akad. d. Wissensch., Math-phys. Klasse, Bd. 103, Abth. 1, Wien, 1894; *ibid.* Bd. 104, 1895; also Jahrb. f. wiss. Botanik, Bd. 30, 1897.

The mechanics of the secretions commonly taking place on the surface of stigmas are probably identical with those of nectaries, although it must be seen that the first secretion of sugar, and of the water which carries it, may in both cases be accomplished by active pressing out of these substances by the living cells forming the surface of the gland. When sap-pressure is high in the body of the plant or in the root-hairs themselves, the dissolved substances passing out through root-hairs may be pressed out mechanically by the vital activity of the living protoplasm, as well as by the difference in the osmotic pressures within and without the cell (page 125).

The substances passing out exosmotically or by other pressure from the cells are seldom, if ever, such as contribute directly to the formation of protoplasm. Proteids, albuminoids, and the like, remain in the cells in spite of the differences in proportional composition of the liquids within and without the cells. Though some of these substances may be soluble, none is freely diffusible. According to the differences in diffusibility, soluble substances have been divided into crystalloids and colloids, respectively substances readily and tardily diffusing. It is now known, contrary to former supposition, that colloids may crystallize. For this reason the names are inapt and misleading. The hypothetical explanation of the feeble diffusibility of colloidal substances is this: the molecules of these highly complex compounds are so large (*e. g.* egg-albumen, which, according to Lieberkuhn, may have the formula $C_{72}H_{322}N_{52}O_{66}S_2$*) that they cannot pass through the spaces between the molecules, or groups of molecules, of other substances. On the other hand, a colloidal membrane is no bar to the diffusion of crystalloids, for though its molecules and groups of molecules are large, it is supposed that the spaces between are large enough for smaller molecules to pass through. Thus, apart from Hertwig's conception (p. 7) that the living protoplasm is a definite structure and not a substance or mixture of substances merely, we have a reason why the protoplasm, while permitting the free passage of water and of the substances dissolved in it, remains enclosed within the cell-wall, although by the absorption of much water, or for other reasons, the density of the protoplasm may be greatly reduced.

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* Loew and Bokorny. Die chemische Kraftquelle im lebenden Protoplasma. Munich, 1882.

In this sense the living cell is an apparatus that permits endosmosis while preventing exosmosis. In addition to the failure of protoplasmic (*i. e.* of colloidal) substances to pass through the cell-wall because of the size of their molecules, the living protoplasm (see p. 107) prevents by its bounding membranes the exosmosis of dissolved coloring and of some other substances contained in the vacuoles.

SAP-PRESSURE AND BLEEDING

The transfer of single cells containing osmotically active substances in abundance—for example, ripe pollen-grains—into pure water, or to an aqueous solution of too low density, will cause the cells to swell and finally to burst, in consequence of turgor-pressure which finally ruptures the cell-walls. Such cells would not swell and burst in air, or in a solution nearly or quite equalling the cell-sap in density. Similarly, the accumulation of osmotically active substances in some of the cells of a multicellular plant which can absorb water in abundance, will result in developing pressure—turgor-pressure—in those cells. These, exerting pressure upon neighboring cells, will transmit the mechanical force, often for a considerable distance, and it may ultimately be exerted directly upon the soil or other material surrounding the plant. The materials causing the development of pressure may pass by osmosis to the cells against which pressure is exerted. Thus, though the pressure in one cell or several may thereby be reduced, the means of developing turgor will be extended and the total pressure of the organ or of the plant may remain the same. The turgor-pressure may also be reduced by the living cells which abut on the lifeless ducts and tracheids, pressing out water into these otherwise empty shells. Continuing this process of excretion into the wood elements may result in pressure developing in them also. This pressure in lifeless cells may justly be called *sap-pressure* in distinction from turgor-pressure, which is possible only in living cells or in an apparatus similarly constructed.

Perennial plants in temperate climates exhibit all of these phenomena each year with the return of spring. When there are again sufficient warmth and water, the cells in which starch and other reserve foods were stored for the winter are awakened to new life, and form enzyms needed to convert the starch and other insoluble solids into soluble ones. These go into solution in the cell-sap, which thereby increases in density and in osmotic potential. The cell-sap in this condition rapidly absorbs water and, tending to increase proportionally in volume, develops a pressure equal to the force needed to keep it at that volume. This pressure will necessarily be exerted upon the adjacent cells, will thus be extended from cell to cell, the substances dissolved and the water dissolving them will pass by osmosis in the same directions, *i. e.* in the directions of least resistance, mechanical or osmotic. Thus the local pressure will be reduced and the danger that the cells may burst will be removed. The total pressure may remain the same, or the local pressure may become so distributed and equalized that in the plant as a whole there will be none. This last is accomplished whenever water is given off, as vapor or liquid, from the surface of the plant in amount equal to that absorbed.

The ratio between water absorbed and water given off indicates whether there can be any pressure of the cell-sap in any living cell (turgor-pressure) or in the whole plant (sap-pressure). The greater the absorption in proportion to the loss of water by evaporation, transpiration, or secretion, the greater the pressure, local and general; conversely, the greater the loss of water in proportion to the absorption the lower the pressure, local and general. Copious absorption is dependent upon the presence in the cells of a large amount of soluble and osmotically active substance and upon the presence outside of a large amount of water. Small loss of water is dependent upon small surface, upon the impermeability of the walls of the superficial cells, and upon low protoplasmic activities in them. These conditions are met especially in spring, but also to a limited extent during and immediately after rain in summer. In spring, water is taken up in quantity from the moisture-laden soil by the dense cell-sap of the root cells; from the still bare branches and the unopened buds water is given off only in very small amount;* sap-pressure develops in consequence.

If a plant in this condition has been so recently trimmed or pruned that the wounds are not yet closed, or if new wounds are opened, we shall have the familiar phenomena of "bleeding" and of sap-flow. The name "bleeding" or "weeping" is given to wholly useless if not injurious exhibitions of the phenomena, employed by the farmer in northern North America when he "taps" his maple trees in spring to secure the highly prized maple syrup and maple sugar. What flows from the plant, whether in bleeding or in the run of sap after tapping, is the water expressed into the wood elements by the living cells bordering upon them. This sap, flowing out under pressure, is a solution containing various organic compounds—in maple chiefly sugars—and mineral salts. The presence of mineral salts in the sap, and their accumulation in the evaporating pans employed in sugar-making, are due to their being taken up, a little at a time, by the plant in the water absorbed from the soil. The amount and the kinds of salts present in the sap will vary with the nature of the soil and with the kind of plant, for the reasons which we have above considered (p. 112). The amounts and the kinds of organic matters will vary not only with these two factors, but also with the condition of the individual, both at the time, and during the foregoing season, when organic substances were being formed and stored by the plant.

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* It is not a question of surface merely, however, for in evergreens, although the surface is not materially less in winter and spring than in summer, the amount of water given off during winter and spring is much less than in summer. The lessened activities of the protoplasm in leaves and branches, and the decreased evaporation at the lower temperatures, account for this.

Sap-pressure, which determines the rate of sap-flow and of bleeding, varies at different times in the season and in the day. The amount of water in the soil and of moisture in the air will directly affect the physical conditions of sap-pressure and of sap-flow. If the soil is dry, only small amounts of water can be absorbed, the turgor-pressure in the living cells of the root will be relatively low, comparatively little water will be pressed from these cells into the wood-elements, and therefore the sap in the wood will increase proportionally little in volume and pressure. If the air is dry, more water will evaporate from the plant, the ratio between the amounts absorbed and given off will be lowered, and the volume and pressure of the sap in the wood will be proportionally lowered.

Other factors, acting directly upon the protoplasm and only by this means affecting the physical conditions of sap-pressure, cause the pressure and rate of flow to vary from time to time. Whatever stimulates the protoplasm of those cells in which food is stored in solid form to dissolve the food, will tend, other things being equal, to raise the sap-pressure by increasing the absorption of water and the turgor-pressure. The increased secretion by the protoplasm of diastatic or other enzyms, by means of which more insoluble solids will be converted into osmotically active soluble substances, increases the absorbing power of the cell-sap and proportionally increases its volume and pressure. Conversely, whatever influences depress the protoplasmic activities also tend to reduce the sap-pressure.

Experiments by Wieler* on plants in pots, and therefore under controllable though somewhat artificial conditions, confirm the observations made on plants in nature* that low temperatures (freezing or lower) decrease the sap-pressure and the sap-flow and may stop the bleeding. With a rise in temperature the pressure will rise and sap-flow will be resumed. Experience shows that cold at night, stopping the sap-flow, and warmth by day, causing it to be renewed with vigor, are most favorable to a copious yield of sap of good quality.

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* **Wieler, A. L. Das Bluten der Pflanzen. Cohn's Beiträge zur Biologie der Pflanzen, Bd. VI., 1893. Gain, E. Action de l'eau du sol sur la végétation. Révue Générale de Botanique, t. VII., 1895.**

The means of measuring the pressure developed by the absorption of water are at the best inadequate, for the various forms of pressure-gauges (manometers) employed cannot be made to measure the total amount of force developed. A manometer measures merely the *net* force. Each individual cell which is restrained from expanding, and which absorbs more water than it gives off, exerts force, develops pressure. But by no means all the cells of a plant develop pressure simultaneously; some cells develop no more than average pressure, and some dead parts (*e. g.* ducts, tracheids, etc.) cannot develop osmotic pressure under the conditions ordinarily prevailing in the plant. Against these less resisting cells those under pressure and seeking to expand, exert force. This force, being partly or wholly unresisted, expends itself, the pressing cells expand, the others collapse. Again, water may be forced into tracheids and ducts by adjacent cells and thus the pressure of the latter will be reduced. If, however, tracheids and ducts become *filled* with sap, as is the case in early spring in the sugar maple, vine, etc., pressure will develop in these dead parts also, because of the force exerted by the osmotically active living cells, adjacent or more or less remote. The pressure developed by one group of cells may, then, expend itself wholly in some other part of the body of the plant, leaving no force to be exerted upon the pressure-gauge. The pressure-gauge indicates only that amount of force due to sap-pressure which is not expended in the body of the plant itself, that is, the *net* force as it may be called, to distinguish it from the total force.

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* **Bibliography in Wieler's paper above and papers by Jones and Orton, Sap-pressure and flow in Sugar Maple. Ann. Report Vermont Agric. Exp. Station, 1898. Morse and Wood. Studies of Maple Sap. Bulletins 24, 25, 32, New Hampshire Coll. Agric. Exp. Station, 1895.**

In spite of the inadequacy of the means for measuring sap-pressure, figures of very considerable magnitude are to be found in the published studies on this subject. For example—

in Ricinus communis	6⅓	lbs.	to	sq. in.
Urtica dioica	9¼	"	"	"
Vitis vinifera	21⅓	"	"	"
Betula alba	28	"	"	"

Strangely enough, since the researches of Clark* in 1873, little attention has been paid in this country to the phenomena of bleeding, in spite of the facts that the important maple-sugar industry depends upon it, and that there are botanists at the Agricultural Experiment Stations of the sugar-making States.

For the very natural but also very poor reason that sap-pressure has often been measured on the stumps of small plants cut off near the ground—that is, where the sap-pressure must develop almost wholly within the root—it has been commonly called *root*-pressure. That this is a misnomer follows not only from the foregoing consideration of the physics of sap-pressure, but also from the introductory experiments of Pitra,† repeated and extended by others, upon the sap-pressures which may be developed in parts above ground, for example, branches cut off from the main stem and thus wholly separate from the root. The sap-pressure of such amputated parts may even be higher than of those left attached to the root. It is true that the sap-pressure develops first in the lowest parts and gradually ascends the stem or branch, but this is owing to the absorbing part being below. It is the roots, or the lower ends of amputated branches, which absorb the water, and it is necessarily the cells nearest the absorbing parts that first develop pressure and from which, after a time and after the pressure goes beyond a certain height, sap is pressed out into the tracheids and tracheæ to make room for the water which continues to be absorbed. Although the sap-pressure is generally greatest at the base of a stem or the butt of a branch, the pressure is clearly due to a condition in some group of cells, whether these are in the root or elsewhere. We should, therefore, abandon the misleading name of root-pressure and use only the equally self-descriptive but correct term sap-pressure.

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* Clark, W. S. Circulation of sap in plants. Lecture before Mass. State Board of Agriculture, 1874.

† Pitra, A. Versuche über die Druckkraft der Stammorgane bei den Erscheinungen des Blutens und Thränens der Pflanzen. Jahrb. f. w. Botanik, Bd. XI., 1877.

The amount of sap-flow is exceedingly different, not only for different species and different individuals of the same species, but also for the same individuals in different seasons. The reasons for this diversity we have already considered. The following figures will serve to indicate the volumes sometimes obtained—

Birch	**in 7 days**	**yielded**	**36**	**liters sap**	**(Wieler)**
(12 years old)	**daily average**		**5+**	**" "**	
Agave	**"**		**7.5**	**" "**	**(Humboldt)**
(decapitated flower stalk)	**in 4-5 months**		**995.0**	**" "**	
Sugar maple	**in 23 days**		**93095.0**	**grs. "**	**(Morse)**
(trunk 7 ft. circumference.)	**daily average**		**4047.0**	**" "**	
			=3.6	**litres "**	
					(Sp. gr. 1.32)

TRANSPIRATION.

From all their surfaces exposed to the air, plants give off water-vapor. This is a physical necessity, for water-vapor will be given off from any mass, lifeless or living, which contains water, whenever the surrounding air is not saturated with moisture, or when the mass has a temperature higher than that of the air, or when the mass, in relatively dry air, is not enclosed in a waterproof covering. Other things being equal, the amount of water-vapor given off will be greater the greater the exposed surface in proportion to the mass. With like conditions of humidity, temperature, surface-composition, and surface-area, equal masses of different composition will dry, *i. e.* lose water by evaporation, at different rates, a gelatinous or slimy mass more slowly than a woody one, for example. The living plant differs from a dead one of exactly the same dimensions in being able to control four of these five factors, and to that degree it is able to control the rate and the amount of evaporation. Because evaporation from the body of the living plant is controllable within certain limits by the plant itself, and to this extent is a physiological process, it has been given the separate name of *transpiration*. With this idea of evaporation controlled by the living organism has been coupled the notion that water is vaporized by the chlorophyll grains illuminated by sunlight and manufacturing carbohydrates, and that this water-vapor, produced by physical means acting through the living organs of the plant, is an important part of the total volume of water given off. This process Van Tieghem* distinguishes from evaporation by the name of *chlorovaporization*. Assuming that water is set free in combining carbon-dioxide and water into carbohydrate, it is hard to conceive that the liberation of water in a water-containing cell would be in the form of escaping vapor any more than in the familiar reactions carried on in solutions in the laboratory. The water molecules liberated at the temperatures prevailing in cells photosynthetically active would mix with the water in the cell-sap both in the protoplasm and in the vacuoles. Because light is absorbed in chlorophyll-containing cells, the temperature of these cells may be (but not necessarily will be) higher than of other cells not absorbing light. If this is the case, and if these cells are warmer than the air, evaporation will of course take place. Transpiration is, therefore, a physical process controlled but not carried on by the living plant. According to circumstances it may be more or less rapid than simple evaporation.

Plants living in regions where the rain-fall is slight or is very unequally distributed through the year, and where the soil is not an efficient reservoir of water, are forced not only to store water in their bodies (see p. 124) but also to check the loss of water by every possible means. The greatest economy of water is shown by the Cacti. In the most condensed forms we have nearly spherical plants, the outer surface of which is rendered as impermeable as possible to water and water-vapor by the waxy covering of the outer walls of the epidermal cells, by greatly thickening and cutinizing these walls, by forming more than one layer of epidermis, by sinking the guard-cells of the stomata to the second layer of epidermis, by greatly reducing the number and size of stomata, and in some cases by forming a woolly covering of dead hairs which still further insulates the tissues within. From such plants the loss of water is slight in proportion to the mass, less in proportion to the surface, least in proportion to the amount of water contained in the plants. Evaporation from these plants is reduced to the minimum, transpiration is lowest in rate and in volume, *first*, by reason of the composition of the plant-body, slimy and gelatinous materials holding water, and water-storing tissues, forming a considerable part of the volume of the plant; *second*, by the area, composition and covering of the surface; *third*, by the small number of openings through the insulating covering; and *fourth*, by the body-temperature of the plant being lower than that of the air when the air could otherwise take up most moisture.*

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* Van Tieghem, Ph. Traité de Botanique, t. I., p. 185, 1891. Also Transpiration et chlorovaporisation. Bulletin de la Soc. Bot. de France, 1886.

The opposite extreme is represented by plants living in the very humid regions of the tropics. There the air is always near the point of saturation, and the almost daily showers at certain seasons attest both the frequency with which the air attains the point of saturation and also the great amount of moisture which can be quickly precipitated. The well-known copiousness and frequency of the tropical downpours indicate that great volumes of water must somehow be vaporized. It has sometimes been concluded, from the tardy evaporation of water from wet masses having the same temperature as the surrounding air, that all tropical plants must have other means than transpiration for getting rid of the water absorbed by them. Some do have other means in the hydathodes (p. 128), but not many plants are so equipped. Whenever the temperature of the plant is higher than that of the moisture-saturated air outside, transpiration will take place, the water-vapor condensing on the surfaces of the plant and elsewhere. Because the plant in its respiration has a means of developing heat, it must often be the case in the tropics that the plant is warmer than the surrounding air. That transpiration into the moisture-laden air of the tropics is sufficient for getting rid of water is evident when we take into consideration the following matters. *First*, the plant absorbs water because it needs and uses both water and the salts dissolved in it. Of the salts it needs only very small amounts, as shown by culture experiments, and though analyses of the mature plant may reveal the presence of much larger amounts of some or all of the useful salts, it does not by any means follow that these amounts are used, or, if they are used, that the plant is not over-fed. Of the water it needs enough to bring adequate amounts of the indispensable salts, and if the plant absorb enough water for this purpose, it will certainly have sufficient for all other purposes also, because the solutions of needed salts are so dilute. In certain places one of the advantages attained by transpiration certainly consists in the lower body-temperature of the plant, since vaporization is a cooling process. *Second*, transpiration even into a very humid atmosphere will sufficiently concentrate the cell-sap of superficial cells to ensure an osmotic current into these cells, supplying them with both the water and the salts which they may need. *Third*, no more water will be absorbed than the plant needs, for the living cells control by their activities those physical conditions which make absorption possible. If the transpiration of plants living in the humid tropics is less than of plants living in drier regions, the absorption of water will be less. So long as water and needed salts are absorbed in sufficient quantities, growth and the other activities of the plant will be normal. The luxuriant vegetation of the tropics impresses every one with the idea that there growth, food-manufacture, etc., must be more rapid and more abundant than in temperate regions. The correctness of this view is questioned by Giltay,* at least so far as food-manufacture is concerned. On equally fertile soil in equal lengths of time, the activities of tropical and temperate plants are not unlike. If this is true, there is no need of more rapid absorption and transfer of food in tropical plants than in those of temperate climes, and transpiration may at least be no more rapid, may safely be less rapid, than in dryer temperate regions. It may easily happen in temperate regions that the plant takes in more water and more salts than it really needs, and that while the former evaporates, the latter accumulate in useless forms and quantities with or without chemical change. Whether the transpiration of plants adapted to the climatic conditions of different parts of the world differs greatly must be regarded as still unsettled.†

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* For a further discussion of these interesting adaptations consult Goebel, Pflanzenbiologische Schilderungen; Volkens. Flora der ägyptisch-arabischen Wüste, 1887; Schimper. Pflanzengeographie auf physiologischer Grundlage, 1898.

The result of the evaporation of water from any solution is the concentration of the solution and the lowering of its temperature. With the evaporation or transpiration of water from the leaves of plants, the cell-sap of the cells giving off water will tend to increase in density and to decrease in temperature at a rate proportional to the rate of transpiration. The increase in density of the cell-sap is accompanied by an increase in osmotic pressure, and the cell-sap draws water from adjacent cells with corresponding force. The decrease in the water-content of the parenchyma cells causes a greater draft upon the water-conducting tissues not only adjacent but throughout the conducting system, for a draft upon one part disturbs the balance throughout the whole. Thus, assuming an adequate force by which water is raised through the ducts from root to leaves, we see that this force is set in motion, and its action is regulated, by the amount and the rate of transpiration. Transpiration must then also affect the root-hairs, regulating the amount of water which they absorb. A current—for parts of its course osmotic, for the remainder of much larger dimensions—is set up, maintained and controlled by transpiration. Transpiration is, however, only one means of doing this, water-pores (p. 128) and hydathodes (p. 128) being the others, and perhaps equally important for the plants which possess them.

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* Giltay, E. Über die vegetabilische Stoffbildung in den Tropen und in Mitteleuropa. Annales du Jardin Botanique, Buitenzorg, t. XV., 1898.

† The discussion of the question is represented by the following papers: Haberlandt, G. Anatomisch-physiolog. Untersuchungen über das tropische Laubblatt. I. Über die Transpiration einiger Tropenpflanzen. Sitzungsber. d. K. K. Akad. d. Wiss. zu Wien, Bd. CI., Abth. I., 1892. Über die Grösse der Transpiration im feuchten Tropenklima. Jahrb. f. wiss. Botanik, Bd. 31, 1898. Erwiderung zu Giltay's Abhandlung. Jahrb. f. wiss. Bot., Bd. 33, 1899. Stahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung, 1894. Burgerstein, A. Über die Transpirationsgrösse von Pflanzen feuchter Tropengebiete. Ber. d. Deutsch. Bot. Gesellsch., 1897. Materialien zu einer Monographie betreffend die Erscheinungen der Transpiration der Pflanzen. Verhandl. d. K. K. Zool.-Bot. Gesellsch., Wien, 1901 and earlier. Giltay, E. Vergleichende Studien über die Stärke der Transpiration in den Tropen und im mitteleuropäischen Klima. Jahrb. f. wiss. Botanik., Bd. 30, 1897. Die Transpiration in den Tropen und in Mittel-Europa, II., Jahrb. f. wiss. Bot., Bd. 32, 1898; *Ibid.*, III., *loc. cit.*, Bd. 34, 1900; *Ibid.*, Bot. Centralbl., Beihefte, Bd. 9, 1900.

The ordinary means by which evaporation is controlled by higher plants are two: *first*, the stomata (p. 142), which control the exchange of gases as well as of water-vapor between the plant and the air; *second*, the character of the epidermal and other cells (cork, etc.) covering the plant.* Special means of facilitating or checking transpiration are possessed by plants inhabiting especially damp or especially dry regions.†

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* Consult De Bary, A. Comparative anatomy of the vegetative organs of phanerogams and ferns. Oxford, 1884.

† These topics need not be discussed here. They illustrate no new principles in plant physiology. The following papers may be read by the interested student. Other papers and books have been referred to in the preceding pages. Stahl, E. Regenfall und Blattgestalt. Ann. du Jardin Bot. de Buitenzorg, Bd. XI., 1893. Über bunte Laubblätter. *Ibid.*, Bd. XIII., 1896. Kny, L. Zur physiologischen Bedeutung des Anthocyans. Atti del Congresso Botanico Internationale, 1892. (Older literature here cited.) Keeble, F. W. The hanging foliage of certain tropical trees. Annals of Botany, vol. IX., 1895. Darwin, Charles and Francis. The Power of Movement in Plants, 1880. Stahl, E. Über den Pflanzenschlaf und verwandte Erscheinungen. Botanische Zeitung, I. Abth., Heft. V., VI., 1897. Wilson, W. P. and Greenman, J. M. Preliminary observations on the movements of the leaves of Melilotus alba L. and other plants. Contrib. Botan. Laboratory, Univ. of Pennsylvania, 1892.

STOMATA AND THE AERATING SYSTEM

The preceding paragraph leads us to a consideration of those special epidermal structures, the stomata, which are the chief means by which the plant controls the transpiration of water-vapor and the exchange of oxygen and carbon-dioxide. The stomata are the guarded openings, on the surface of the plant, of those intercellular spaces which form throughout its body a system of continuous passages through which gases, passing diosmotically into and out of the adjacent living cells, make their way from and to the outside air.

Through open stomata and intercellular passages gases can diffuse more rapidly than they can pass by osmosis through cell-walls soaked with water. Besides the uninterrupted diffusion which these passages and openings make possible, still more rapid movement of enclosed gases and vapors must take place whenever the plant is agitated, swayed by the wind, or by passing animals. Even changes in the positions of the organs of the plant, resulting in changes in the diameter of the intercellular spaces in one region and a consequent change in the equilibrium of the enclosed gases and vapors, will facilitate the movement of gases throughout the whole aerating system. Thus the constant trembling of the leaves of the aspen (*Populus tremula*, and *P. tremuloides*), and often of other plants also, in the slightest breeze, and the autonomic movements of the leaflets of *Desmodium gyrans* are claimed by Stahl* to increase transpiration. If they do this, they must also accelerate the interchange of gases.

The intercellular spaces which, uniting together, form with the stomata the aerating system of larger massive plants, are of very different sizes according to their position and according to the needs of the cells enclosing them. Between the chlorophyll-containing, food-making cells of the leaf the intercellular spaces are comparatively large. In the leaves of plants growing in damp places they are even larger than in other leaves.[*] The large size is due to the need of getting rid of water-vapor as rapidly as possible, and of obtaining sufficient quantities of the carbon-dioxide contained in such minute proportions in the air. There must, therefore, be a rapid passage of comparatively large volumes of air past these mesophyll cells. On the other hand, the intercellular spaces in the deeper tissues, where the cells demand mainly, if not exclusively, the much more abundant oxygen, are relatively very small. Merismatic tissues—for example, cambium—enclose no intercellular spaces, and though aerated only osmotically, they obtain oxygen in sufficient quantities from the adjacent tissues which do enclose air passages. Hollow stems—such as those of the grasses—and dead cells are filled with air, but these are not to be regarded as forming part of the aerating system. On the contrary, they merely contribute, like the air chambers, bladders, etc., of water-plants, to the lightness of the organism.

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* Stahl, E. Über den Pflanzenschlaf und verwandte Erscheinungen. Bot. Zeitung, 1897.

The cells enclosing the air spaces have walls which are freely permeable to water-vapor and to gases. Because these cell-walls, like all others in the plant except those forming the outermost bark-layers, are saturated with water, the passage of oxygen, carbon-dioxide, and nitrogen (if this is taken up at all) through them must be in solution, by osmosis, just as salts enter the cells. The cell-walls bordering upon the unconfined air, however, are so modified chemically by cutinization, suberization, and various impregnations (*e. g.* with SiO_2), and by being overlaid with wax, that they are far less permeable to gases and still less to water-vapor. The slow exchange of gases through epidermis with closed stomata or with none has been repeatedly demonstrated,[†] most recently and certainly most simply, however, by the use of dry filter paper impregnated with cobalt chloride and by the iodine test for starch.[‡] It is well known that cobalt paper, blue, when dry, will change to a pink hue when exposed to dampness. This fact has been employed by Stahl in demonstrating that transpiration through the walls of epidermal cells is much slower than through open stomata. The iodine test for starch demonstrates whether carbon-dioxide enters the leaf through cell-walls in sufficient quantities for starch manufacture. In most plants the epidermal walls are too impermeable for this.

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[*] Stahl, E. Einige Versuche über Transpiration und Assimilation. Botanische Zeitung, 1894.

[†] See discussions of this in Pfeffer, Pflanzenphysiologie, I., §§ 21, 29, 30. Engl. transl., vol. I., §§ 21, 29, 30.

[‡] Stahl, E. *L. c.*

Through the relatively impermeable superficial tissues—epidermis and cork—there must evidently be openings of the intercellular aerating passages. The most important and the most perfect of these openings are the stomata, found on leaves and other young parts. On older and persisting parts the enclosing cork layer may be interrupted by lenticels—masses of rounded cells, unchanged as to their walls, and enclosing intercellular spaces continuous with those deeper in the body of the plant. Cork may be replaced on submersed organs, or on those growing in the mud of swamps and marshes, by a homologous tissue, like that composing the lenticels, and called *aerenchyma.** Lenticels can be closed, and the passage of gases through aerenchyma can be stopped, only by the growth of new tissue, of cork, which seals the openings. The stomata, on the contrary, are intercellular spaces bounded by a pair of delicately balanced, and in most cases freely movable, epidermal cells. Lenticels are found especially in the bark of stems and branches, though also on older bark-covered roots. Aerenchyma is found almost exclusively on roots. These organs secure mainly the entrance of oxygen in sufficient quantities into the older and not necessarily very active tissues, and at the same time the exit of carbon-dioxide. When they occur on aerial organs they of course facilitate transpiration. Stomata, on the contrary, form most abundantly in the epidermis immediately covering chlorophyll-containing cells.

Oxygen forms about twenty per cent. of the atmosphere and carbon-dioxide one-twentieth of one per cent. The chlorophyll-containing cells must be very active during the hours when they are supplied by sunlight with the energy necessary for photosynthesis. Other cells can work at a slower rate and still accomplish as much, for, being independent of light, they can work longer. These constitute some of the reasons for the position and for the number of stomata.

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* Schenck, H. Über das Aerenchym: ein dem Kork homologes Gebilde. Jahrb. f. wiss. Botanik, Bd. XX., 1889.

Stomata are sometimes called "breathing pores." They do admit oxygen, and whenever respiration exceeds photosynthesis (*e. g.* in the dark), the unused carbon-dioxide may pass out through them. For these reasons they are breathing pores, but this is neither their sole nor their main function. Through open stomata water-vapor passes outward and carbon-dioxide inward. Through the stomata on the surface of the parts of the flower, little carbon-dioxide passes inward, for these are not food-manufacturing organs. On the contrary water-vapor and expired carbon-dioxide pass outward. On such organs the stomata are essentially organs for increasing and controlling transpiration.*

A stoma consists fundamentally of a pair of epidermal cells not completely connected together and, therefore, either constantly separated from each other by a slit-like space, or separated whenever the cells draw or are drawn apart. The pair of incompletely connected cells—known as guard-cells—are usually strikingly different in size, form, and contents from other epidermal cells. The cells immediately adjacent to them may also depart from the type of epidermal cells both in appearance and in function. Such cells when present are known as accessory or auxiliary cells, for they either supplement the guard-cells in their task of opening and closing the stoma, or they themselves open and close the stoma by drawing the guard-cells apart or pushing them together. Strictly speaking, the stoma is the slit-like opening (*Spaltöffnung*) between these cells, just as the mouth is the cavity opened and closed by the lips.

The opening and closing of stomata are accomplished by physical means only, but these means may or may not depend upon the irritability of the living protoplasm of the guard-cells and auxiliary cells. Fundamentally, the opening and closing of the stomata are due to changes in the turgor,* consequently in the form and dimensions, of the guard-cells. These changes in turgor may be due wholly to the absorption and withdrawal of water by means only remotely if at all controlled by the living cells, or they may be due to stimulations of the living cells which cause them to absorb or to expel water or otherwise to change the density of their cell-sap with consequent changes in turgor. The accompanying figures illustrate a stoma without auxiliary cells (Fig. 3) and with auxiliary cells (Fig. 4). From figures 5 and 6 the differences in thickness of the different walls of the guard-cells are evident. The thin walls joining the guard-cells to their neighbors permit rapid osmotic transfer, the thin walls opposite are pliant. If, for any reason, the guard-cells absorb water, the volume of the cell cavities will increase, the form of the cells will change, and they will occupy the position indicated by the heavy outline in figure 5; the stoma will be open. If the reverse is the case, if the amount of water in the cell-sap is diminished by evaporation or expulsion, the volume of the cell cavities will decrease, the thin adjacent walls of the guard-cells will bend out, approach each other and finally come into close contact; the stoma will be closed. From the figures it will be noticed that the guard-cells, provided

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* Chester, Grace D. Bau und Function der Spaltöffnungen auf Blumenblättern und Antheren. Ber. d. Deutsch. Bot. Gesellsch., Bd. XV., 1897. Older literature here cited.

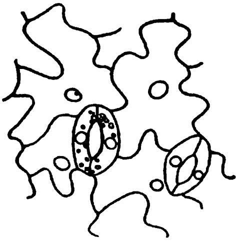

FIG. 3.

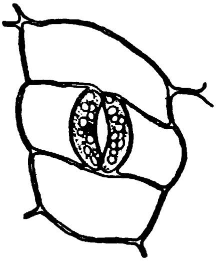

FIG. 4.

Figure 3. Lower epidermis from leaf of *Vicia faba*—showing stomata without auxiliary cells. Figure 4. Lower epidermis from leaf of *Tradescantia zebrina*—showing stoma with auxiliary cells.

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* Mohl, H. von. Welche Ursachen bedingen die Erweiterung und Verengung der Spaltöffnungen? Bot. Zeitung. 1856.

with chlorophyll grains, are capable of manufacturing for themselves substances which are osmotically active, contributing to the turgor as well as to the nutrition of the cell. The other epidermal cells of most plants, being devoid of chlorophyll, must absorb from their neighbors the osmotically active substances upon which their turgescence depends. But their turgescence will vary according to the proportion sustained between the amounts of water which they absorb and give off. If, as is shown in figure 4, the shape, size, position, and other characters of some or all of the epidermal cells adjoining the guard-cells are different from the other epidermal cells, their turgidity will vary at times, at rates, and in degrees different from the ordinary epidermal cells. With these changes in the turgor of the ordinary epidermal cells, of the auxiliary, and of the guard-cells, there will necessarily be changes in the size of the openings, in the degree to which the stomata are open or closed. As recently re-stated by Darwin,* in opposition to the extreme view prevailing of late that the guard-cells alone effect the opening and closing of the stomata, "the pressure of the guard-cells and that of the surrounding epidermis should be looked at as correlated, not as opposed and independent

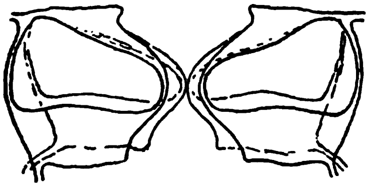

Fig. 5.

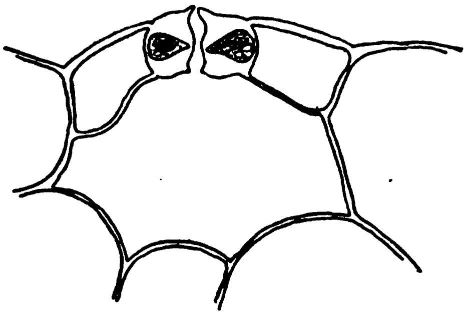

Fig. 6

Figure 5. Diagram (after Schwendener) to illustrate changes in form of guard-cells in opening and closing stomata. Figure 6. Cross section of stoma of *Tradescantia zebrina*, showing relations of auxiliary cells to mechanics of opening and closing.

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* Darwin, Francis. Observations on Stomata. Philos. Trans. Royal Society of London, Series B, vol. 190. 1898.

factors." Yet it is easily conceivable owing to the different rates at which water may be absorbed or given off by the different cells of the epidermis, that in some plants, or under certain conditions of culture, etc., there may be such different conditions in the epidermal cells that while the guard-cells may be expanding and so tending to open the stoma, the other epidermal cells may also be expanding and so tending to push the guard-cells closer together and to close the stoma.* According to Benecke,† the auxiliary cells assist in the opening and closing of the stomata only indirectly and by neutralizing the mechanical strains brought to bear on the guard-cells by the changes in form of the epidermal and even of other leaf cells.

Granting that changes in the turgor of epidermal cells, and especially of those peculiar epidermal structures, the guard-cells, bring about the opening and closing of the stomata, we must enquire how these changes are effected and what are the results as regards transpiration.

Whenever a cell loses more rapidly than it absorbs water, the turgor of the cell will decline proportionally. This difference will occur whenever a cell is unable to supply itself, directly or through its neighbors, with water enough to make good the loss by evaporation. The decrease in turgor of the guard-cells of the stomata, and their consequent flattening, are the result of such external conditions; the stomata are closed. The difference in the amount of water-vapor given off from leaves with open and with closed stomata has been estimated by various means. The most striking way of demonstrating this is perhaps Stahl's cobalt paper method.‡ Leaves with closed and with open stomata are compared, under as like conditions as possible, as to their rates of changing the color of dry filter paper impregnated with cobalt chloride. Whereas the sheet of cobalt paper placed against the leaf with open stomata will change within a few seconds from blue to pink, the color remains unchanged for an hour or more (with *Tradescantia zebrina* for four hours) in the paper in contact with the closed stomata. In spite of the very minute size of the opening, even at its fullest extent, the great number of stomata give us some idea of the effectiveness of these gates at the entrances of the intercellular passages. Pfeffer,* quoting figures as to the size and number of stomata, says the effective area of the opening seldom reaches .0046 sq. mm., but that the number of such openings is from 100 to 300 per sq. mm. Estimating 100 to the sq. mm. at the size .0046 sq. mm., we see that nearly one-half the surface can be opened. Assuming that the stomata are on one side of the leaf only, and that on that side they have the proportions just given, we see that roughly one-quarter of the leaf-surface can be the free path for the exchange of gases and vapors.

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* Stahl, E. *l. c.*, p. 121.

† Benecke, W. Die Nebenzellen der Spaltöffnungen. Bot. Zeitung, p. 602-3, 1892.

‡ Stahl, E. Einige Versuche über Transpiration und Assimilation. Bot. Zeitung, 1894.

The disparity between absorption and evaporation which for physical reasons forces the stomata to close, is often supplemented by the irritability of the protoplasm of the guard-cells. Evaporation insufficient to produce any diminution in turgor visible as wilting may still be enough to irritate the guard-cells into reducing their turgor by physical or chemical changes accomplished in the cells by the living protoplasm. Thus various influences which cannot bear directly upon turgor, but which can irritate the protoplasm, bring about the closing and opening of the stomata. The statements of older authors regarding these influences have been lately tested by Stahl,† and still more recently by Francis Darwin,‡ from whose papers the following conclusions are abstracted. The stomata of most plants are widest open in bright light, less widely open or completely closed in darkness. This one would in general expect, for photosynthesis in chlorophyll-containing cells (and the guard-cells contain chlorophyll) is most rapid in bright light. There would then be the greatest demand for carbon-dioxide to be elaborated into food, and the gateways of the intercellular passages should be open to allow the free entrance of carbon-dioxide. If the stomata close in bright light to guard against excessive transpiration, food production diminishes greatly. The closing of stomata more or less completely in darkness, the decrease in the size of the openings as the light diminishes, may be coupled with these facts: the proportion of oxygen in the air is so much larger than that of carbon-dioxide, and the rate of respiration so much lower than that of photosynthesis (see p. 65), that the stomata may well decrease in size, or even close for a time, without interfering with respiration; transpiration on dry nights might be excessive or at all events would tend to cause in the cells an accumulation of salts unnecessary at the time in amount and kinds; the leaf is cooled by transpiration, and loss of heat by this means might be undesirable; in nyctitropic plants, and in others habitually living where the air is damp, the closing of stomata in darkness is less common than in plants growing under more ordinary conditions. Stomata which have remained closed during the night, begin to open at daylight in the morning. Heat tends to open the stomata. This may have injurious or fatal results. If the leaves of an evergreen, for example of holly, are warmed by air and sun while the roots are encased in soil so cold and dry that the root-hairs absorb too little water, the opening of the stomata is very likely to be followed by excessive transpiration, by the drying out and death of the plant. Indeed, most cases of "winter-killing" are to be attributed to the inability of the plant to balance transpiration by absorption, rather than to actual freezing to death.

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* Pfeffer. W. Pflanzenphysiologie. I., p. 177. Eng. transl., I., p. 195. *Compare also* Brown (Fixation of Carbon, Nature, 1899), *and* pp. 45, 50 of this book.

† *l. c.*

‡ *l. c.*

The majority of plants close their stomata when their leaves are wet. This can be demonstrated by putting in water strips of epidermis from the leaves. The advantage is more obvious than the means by which it is attained. If the stomata are the entrances of the passages through which the necessary exchange of gases and vapor takes place, these entrances must be kept free from whatever would hinder the exchange when the stomata are open.

Rain and dew collecting over the stomata or passing into the intercellular spaces would prevent the diffusion of gases except as they are dissolved in the water. This disadvantage is avoided in the first place by placing the stomata ordinarily on the lower side of the leaf, the one least likely to be wet by rain. It is further avoided by the fact that when the leaf is wet, transpiration virtually ceases while absorption may continue for a time, thus producing such a degree of turgor in the guard and other epidermal cells that their expansion closes the stomata.

Certain plants living in extremely moist places, where the danger of excessive transpiration at any season is reduced to the minimum, are unable to close their stomata. Herbs, shrubs, and even trees (notably the willows) possess this character. It is for this reason that these plants cannot bear transplanting to dryer places for cultivation, but are distinctly swamp plants.

GASES AND THE MOVEMENT OF GASES

If the plant or any part of it dries—that is, loses water faster than it absorbs it—air takes the place of the evaporated water. If the cell-walls and intercellular spaces are equally permeable to gases and to water-vapor, air will pass in as rapidly as evaporation removes the water, but if water-vapor makes its way through cellulose, cuticula and cork faster than air, drying will tend to produce in the plant a gas pressure lower than that of the surrounding air. If again the component gases of the air diffuse and diosmose at different rates, the evaporating water will be replaced by nitrogen, oxygen, and carbon-dioxide in proportions different from those in which they occur in the air. But if the living cells of the plant use any of these gases, the composition of the air in the plant will be influenced by this means also. In all living cells of higher plants under normal conditions oxygen is consumed in respiration and carbon-dioxide is liberated, usually in equal volumes. In all chlorophyll-containing cells carbon-dioxide is consumed and oxygen liberated, under the influence of light. Carbon-dioxide diffuses and diosmoses more rapidly than oxygen, and the latter more rapidly than nitrogen, but these gases make their way less rapidly through drying cellulose and lignified membranes, though more rapidly through cuticula and cork, than does water-vapor. We have seen that the wood, which consists mainly of the walls of dead cells, is the path of the water-currents from root to leaves, that only rarely if ever are the wood elements filled with water, and that generally they contain air and water in alternating columns (Jamin's chains). Whenever transpiration is more rapid than water-transfer, the air-pressure within the plant will decrease; there will be the largest volume of air under the least pressure when transpiration has most reduced the amount of water, and when the vessels are fullest of water there will be the least volume of air under a pressure equal or nearly equal to that of the atmosphere. The constant changes in the rate of transpiration, causing differences in the water content of every cell, living and dead, and in the amount of water-vapor in the intercellular spaces, will cause constant changes in the volume and pressure of the gases within the plant.

More strictly vital activities also affect the gas pressures. As may most conveniently be demonstrated on submersed aquatics, photosynthesis tends, other things being equal, to produce a gas pressure within the plant greater than that outside. Because the stomata of a land plant are usually open while the plant is manufacturing food, the free exchange of gases between the plant and the outside air keeps the pressures about equal. But in submersed aquatics—*e.g.* *Elodea*, *Ceratophyllum*, *Myriophyllum*, etc.—the gas pressure may be made evident in two ways. In the first place, the buoyancy of the plant increases while it is illuminated, indicating the accumulation of gas in its body; and second, the classical experiment of inverting and cutting or pricking the stem* shows that a stream of bubbles, often countable and therefore offering an index of the photosynthetic activity, issues from the cut surface or from the wound. The explanation of this phenomenon of increased pressure is this: the carbon-dioxide used in the elaboration of sugar passes by osmosis more rapidly into the body and into the cells of the plant than the liberated oxygen passes out. The latter, therefore, accumulates in the large and well developed intercellular spaces and passages, escaping only slowly from these by osmosis, escaping rapidly only when the plant is wounded.

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* For description see Darwin and Acton's or Detmer-Moor's laboratory manuals.

The reverse of this result is attained during the night, when the plant is photosynthetically inactive but is steadily respiring, taking in oxygen as fast as it needs it, and giving out the more rapidly diosmosing and diffusing carbon-dioxide. But since respiration is never so active as photosynthesis, the negative pressure is never so high as the positive.

Since plants are subjected to inconstant but frequent movement by the winds, by passing animals, by the rise and fall of the tide, by waves, etc., the gases contained in their bodies are subjected to varying pressures, are forced out and drawn in, are moved from part to part. These mechanical influences brought to bear upon plants play a very important rôle in contributing to the movements of enclosed gases and vapors. Besides these, temperature-changes and, as we have already noted in connection with transpiration (p. 139), the temperature of the plant-body as compared with the temperature of the air outside, also affect the movements of gases in the plant. The effects of these influences, however, are mainly upon the gases enclosed in the intercellular spaces while the other influences which we have considered affect more directly the gases within the cells. But all of these influences contribute to the perfect aeration and ventilation of the plant-body just as the elaborate musculature of the higher animal automatically maintains the movements of the gases needed by the cells of its body. In both animals and plants, osmosis and diffusion underlie all gas movements in the body, but both are controlled by the vital activities, that is, by the amounts of the gases consumed and liberated by the living cells.

From the foregoing it is evident that, in most plants, and under ordinary conditions, the composition of the enclosed gases can differ only slightly and temporarily from that of the surrounding air. In certain species, gas of decidedly and permanently different composition from that of the surrounding air accumulates in chambers of considerable size. As reported in a preliminary paper by Wille,[*] the bladders of the *Fucaceæ* contain absolutely no carbon-dioxide and a varying percentage of oxygen, thus—

Bladders wholly immersed in water contain 35-37% oxygen
" lying for 10 hours in air " 20% "
" darkened for 12 hours " 2.7% "

These figures, in connection with what has just been said about the different diffusibilities of oxygen and carbon-dioxide, are significant. The buoyancy of the plant depends upon its photosynthetic activity and upon the consequent accumulation of oxygen which is collected in specially differentiated reservoirs. Nitrogen necessarily makes up the greater part of the total volume of gas, but this inert gas varies in proportional amount only because of the production of oxygen in photosynthesis and of the consumption of oxygen in respiration during the hours of darkness. So in all plants the proportion of oxygen in the intercellular spaces decreases in darkness, and increases, especially in the intercellular spaces of photosynthetically active tissues, in the light. The impermeability of the cutinized membranes of the epidermal cells of the *Fucaceæ* permits the development of high gas-pressure by means of the abundant production and tardy diffusion of oxygen. Consequently, in spite of their large intercellular spaces, these plants do not collapse even in very deep water.[†] Their buoyancy is thus maintained largely by gas-pressure, and though the form of the cells is maintained by their own turgescence, the form of the whole plant is due to the high gas-pressure in the intercellular spaces as well as to the turgescence and form of its component cells. How much of the size, and to a certain extent of the form also, of plants depends upon maintaining the air-spaces in expanded condition can only be roughly guessed from these figures:[*]

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[*] Wille, N. Abstract, in Just's Jahresbericht der Botanik, vol. XVII., p. 226, 1889, of a "vorläufige Mittheilung," in Norwegian. *Also* Gasarten in den Blasen der Fucaceen. Chem. Centralbl., 1890.

[†] Berthold, G. Über die Vertheilung der Arten im Golf von Neapel. Mittheil. a. d. Zoolog. Station in Neapel, Bd. III., 1882. In this connection it should be mentioned that all seaweeds living between the tide-marks are subjected twice daily to very different pressures. Where the range of the tide is great, as in the Bay of Fundy on the north Atlantic coast, the algæ living near the low-tide mark must adapt themselves to the great differences in pressure.

⅕ to ¼ of the volume of the leaves of most land plants is air-space.

71% of the volume of *Pistia texensis* (a floating plant) is air-space.

3.5% of the volume of *Begonia hydrocotylifolia* (succulent) is air-space.

53% of the volume of the leaf of *Polypodium setigerum*[†] is air-space.

TRANSLOCATION OF FOODS

There remains for us to consider in this chapter the translocation of foods. Through the xylem elements, especially through the ducts and tracheids, aqueous solutions of certain food-materials are transferred from the absorbing root-hairs to the elaborating chlorophyll-containing parenchyma-cells of the leaves. To these same chlorophyll-containing cells the other food-material, carbon-dioxide, makes its way through the stomata and the intercellular spaces. In these cells water and carbon-dioxide are consumed in elaborating a carbohydrate, a food which accumulates in the same or in chemically closely related form in the cells which manufacture it. From these cells the food must be removed, unless it is also to be stored there, to parts needing it at once or in which it can be kept in reserve for future use.

In order to secure the transfer of the non-nitrogenous food manufactured in the green tissues during the hours of daylight, it is usually necessary to change the chemical constitution or composition of the food. If starch or oil is the form in which the carbohydrate elaborated by the chlorophyll-granule is temporarily deposited in the cell, the conversion of these into portable compounds is advantageous. Although oil will pass through cell-wall and living protoplasm, the same amount of nutritious material will pass through the same distance much more rapidly as sugar dissolved in water. Starch, being insoluble, is not only innutritious as such, but is not portable, and hence it must be converted into a soluble substance, also sugar. What is true of the non-nitrogenous foods elaborated in those organs receiving the special form of energy needed for their manufacture, is also true of the nitrogenous foods, elaborated probably in all the living cells of the plant, whether illuminated or not. The nitrogenous foods, if temporarily deposited in insoluble form in the cells elaborating them, will be much more portable if converted into soluble forms. As we have already seen, the non-nitrogenous foods are transferred mainly as sugars, the nitrogenous mainly as amides.

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[*] Pfeffer, W. Pflanzenphysiologie, I., p. 164. Engl. transl., I., p. 182. Various papers there referred to, in which other data may be found.

[†] Estimated from Stahl's figure in Botan. Zeitung, plate IV., fig. 7, 1894. This is a land plant from one of the rainiest regions in the tropics.

We have seen (p. 116) that the transfer of water and dissolved mineral salts from the absorbing organs to those parts in which they are used as food or from which water is evaporated, would be too slow to secure an adequate supply if the movement were wholly osmotic. In order to satisfy the needs of cells consuming food, and to free the manufacturing cells from elaborated food so that they may continue to make it, the transfer of foods must also be by more rapid means than by osmosis merely. In small and simple plants the manufacture, consumption, and storage of food may go on in the same cells simultaneously. In larger plants, division of labor and differentiation of tissues secure greater efficiency and economy. In these plants there differentiates a system for distributing elaborated foods from the places of manufacture. The earliest and simplest conducting system is for this purpose. We find such a system well developed in the large marine algæ (*Fucus, Laminaria, Nereocystis*, etc.). When plants come upon the land it becomes hard to obtain water and easy to lose it. When plants, by becoming erect, limit their water-absorbing part to one end and place their food-manufacturing cells at the opposite end of the body, they must supply themselves with a tissue system for the rapid conduction of water and salts from roots to leaves. The wood, which carries mainly food materials, is so much more conspicuous than the bast, which carries foods, that the wood seems the more important and the earlier needed of the two. This may be true of land-plants, but it is not true of aquatics. Phylogenetically the food-conducting system is the older; in aquatics it is the main or only tissue for the rapid transfer of aqueous solutions.

The anatomical distinctions between wood and bast are so evident that it is easy to infer that there is perfect division of labor between these two sets of tissues. But the living cells of the bast need mineral salts, perhaps to maintain turgor (p. 99), to neutralize injurious by-products (p. 100), to assist in the construction of protoplasm (p. 101)—and will receive, transfer and use them just as the living cells of the wood need sugar and amides as food and will receive, transfer, and consume them.

From illuminated chlorophyll-containing cells the carbohydrates not laid down in solid form like starch or in slowly transferable form like oil, will pass by exosmosis to adjacent cells containing less. Such osmotic transfer will continue while the chloroplastids are manufacturing diffusible food and until osmotic equilibrium has been attained. Osmotic transfer will begin so soon as the carbohydrate deposited as starch or oil is converted into diffusible form, and it will continue so long as starch and oil are converted into sugar. From cell to cell in the leaf parenchyma, and from this into the cortical parenchyma of branch and stem, osmotic transfer will take place; but it will take place always most rapidly in the direction of least osmotic pressure. This will obviously be toward and into the sieve-tubes of the vascular bundles. The sieve-tubes—composed of comparatively large, long cells with thin lateral walls and perforated cross-walls—are continuous for considerable distances, often forming, by means of anastamoses, a system uninterrupted from tip to base of the plant. In the sieve-tubes, as in the ducts and tracheids, there will tend to be less pressure than in the adjacent cells. In the ducts and tracheids the danger of collapse is avoided by the thickened and strengthened walls. In the sieve-tubes permanent collapse always occurs sooner or later (as may be seen at any time in the older parts of the phloem in perennials or late in the season in annuals). It may be produced at any time by cutting off the part—leaf, branch, or stem—whereupon examination will reveal the sieve-tubes and their contents in the abnormal condition figured in even the most recent text-books. Collapse of the sieve-tubes undoubtedly occurs more or less completely, though only temporarily, in the healthy plant whenever the leaf or branch or stem is unduly bent and whenever the removal of food from the sieve-tubes by the adjacent cells for use or for storage is more rapid than the supply of food from the places of manufacture. The pressure in the sieve-tubes will vary, just as pressure varies in any cell, according to the prevailing conditions; but because the sieve-tubes are continuous and are in contact with cells which consume or store as well as with cells which manufacture food, the osmotic and other pressures in them are likely to be lower than in the food-manufacturing cells. Because they are composed of long cells, the cavities of which are continuous with one another through the pores in the cross-walls, the sieve-tubes are especially adapted to the translocation of the osmotically less portable nitrogenous foods, especially the proteids. It would appear from the investigations of Czapek* that it is especially in them, not even in the companion and cambiform cells of the phloem, that the diffusible carbohydrates also are transferred. It does not necessarily follow, from the discovery of minute starch-grains in the sieve-tubes, that they pass as such through the sieve-like cross-walls. On the contrary, starch occurring in the sieve-tubes must be regarded as carbohydrate merely temporarily deposited there after being converted from portable to stationary form. These starch-grains in the sieve-tubes, like the great majority if not all of the solid particles in other cells, are too large to pass through pores in the cross-walls.†

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* Czapek, F. Zur Physiologie des Leptoms der Angiospermen. Ber. d. Deutsch. Bot. Gesellsch., Bd. XV. 1897.

† Sachs, J. von. Lectures on the Physiology of Plants. Engl. trans., p. 325.

The presence of starch-grains in the sieve-tubes has given occasion to the hypothesis that either the sieve-tubes themselves, or their companion-cells, are the chief elaborators of carbohydrates into nitrogenous matters.* Such is, however, hardly likely to be the fact (p. 69). Although very likely the sieve-tubes do form nitrogenous food from nitrates and carbohydrates, this function seems not yet to have been appropriated by any special tissue. Apart from the classical experiments of ringing or girdling plants, with the result that the downward transfer of food is nearly or quite stopped, it must be admitted that exact experiments and definite knowledge on the special functions of the sieve-tubes remain for the future.† The recent discovery by Raciborski ‡ of a substance resembling the hæmoglobin of higher animals in that it readily gives up oxygen to the sieve-cells and lactiferous tubes, in which it regularly occurs, suggests that besides conducting and perhaps contributing to the elaboration of foods, these tissues may also obtain needed oxygen from the substances which they conduct. But as Raciborski says in his second paper, this discovery made in the tropics and away from laboratories must be tested and made the starting-point for research by plant-physiologists with laboratory facilities.

The milk-tubes or lactiferous (laticiferous) tubes or vessels, occurring in a very considerable number of plants and forming continuous systems often as extensive as the sieve-tubes, are filled with a mixture of the most diverse compounds dissolved or suspended in water. Some at least of these substances are the often very useful by-products formed in nutrition, respiration, or in other vital processes. On the other hand, some being subjected to more or less profound chemical changes, serve as sources of energy in respiration, as materials for the construction of cell-wall, and as building-material for protoplasm. Because latex—the contents of the milk-tubes—is composed in part of such nutritious substances as starch, sugars, fats and oils, and proteids, and because the milk-tubes form a system wholly uninterrupted throughout its extent by cross-walls of any kind, the suspicion is irresistible that these tubes offer the easiest course for the transfer of food from part to part. They occur in plants relatively few in number and consequently cannot be indispensable to food transfer. Their functions too need further investigation.

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* **Sachs, J. von. Lectures on the Physiology of Plants. Engl. transl., p. 325.**

† **Trelease (Sixth Annual Report, Missouri Bot. Garden, 1894) finds no sieve-tubes at all in** ***Leitneria floridana.***

‡ **Raciborski, M. Ein Inhaltskörper des Leptoms. Ber. d. Deutsch. Bot. Gesellsch., Bd. XVI., 1898. Weitere Mittheilungen über das Leptomin.** ***ibid.***

The opposite process to that which goes on in the chlorophyll-containing cells of the leaves, whereby the elaborated carbohydrate temporarily deposited as starch is dissolved for transport elsewhere, takes place in the organs where carbohydrates are stored in solid form. In roots, rhizomes, and tubers, in pith and medullary rays, and in seeds, parenchyma cells remove the sugar from the solution in which it comes to them by depositing it as starch grains in the protoplasm or as cellulose lining their walls. How the carbohydrates are acted upon by the protoplasm, or by its special organs the leucoplastids, how sugars are converted into cellulose or into starch and by this means are removed from solution, are still unanswered questions. It is easy to see that if sugar is removed from the cell-sap more will go by osmosis to the cells removing it from solution. This last is a necessary physical consequence of the physiological (that is, in this case, of the combined chemical and physical) action of the living protoplasm. But this storing action of the protoplasm is as little understood as the first secretion of sugar in nectaries (p. 126).

Still less comprehensible at the present time are the accumulations in limited regions of the plant of substances which ordinarily would move osmotically in one direction as readily as in another. The storage of carbohydrate in the form of inulin, dissolved in the cell-sap of dahlia-tubers and in the underground parts of other *Compositæ*, is not to be explained by the ordinary laws of physics. The living protoplasm which, in one part of the plant, elaborates food and permits its exosmosis, accumulates food and prevents its exosmosis in another part. Similarly in the filamentous alga, the accumulation of sugar in its cells bounded on all sides by membranes permeable by water is conceivable only on the hypothesis, strengthened by analogy (p. 107), that the living protoplasm in some way interferes, either physically or chemically, with the exosmosis of the sugar.

To summarize the results of the discussions in this chapter we may say that diffusion and osmosis underlie the processes of absorption and transfer of food-materials and of foods, but that the movements of these gases and solutions, and of the separate substances in the solutions, are controlled in direction, rate, and amount by the living protoplasm. Its needs, and the amount and kind of work it does, change or establish physical conditions and set in operation physical and chemical laws.

CHAPTER V

GROWTH

The processes so far discussed supply the plant with the materials and with the energy to carry on other processes popularly regarded as functions peculiar to living beings, and at all events performed with a greater degree of independence and self-control by them than by lifeless objects. In this respect, however, these processes do not differ from those already examined, for we have seen that respiration is oxidation controlled and, to a certain extent, carried on by the living organism; that nutrition depends upon chemical syntheses accomplished by living protoplasm, which uses simple substances obtained by itself, through its application of the laws of diffusion and osmosis; that the absorption and transfer of food-materials and of foods are physical processes made possible and regulated by the living organism. The processes which we have still to study—growth, irritability, and reproduction—involve and consist in chemical changes not confined to living organisms but controlled by them.

Growth cannot be understood unless the sensibility of the growing substance is constantly borne in mind. A crystal of copper sulphate in a concentrated and slowly evaporating solution of this salt could not grow if the molecules of copper sulphate were not mutually attractive, if those which were still moving freely in the solution did not respond to the attraction exerted upon them by those already settled. The limits of form and size, of rate and direction of growth, of copper sulphate crystals, are fixed by physical laws, but though these laws are universal, the balance in any one spot may be very different from that elsewhere, and the growing crystal will conform and must conform to its environment. It is determined by physical law that copper sulphate molecules will not arrange themselves in the crystalline form without a definite amount of water; if the amount of water be excessive or deficient the copper sulphate molecules, having always the same attraction for one another, will still be unable to obey it, to approach one another, and to arrange themselves in their due order. The crystals of the same substance will be small or large according as they are formed fast or slowly. And what is true of the behavior of one substance alone in solution in another is also true of many substances together in solution, whether these find themselves in a cell or wholly outside a living body. The molecules of the different substances will mutually attract or repel one another, they will be indifferent or they will decompose one another, and when a state of balance is attained, the molecules which result from all the changes will arrange themselves in their characteristic ways. Because the living protoplasm itself is composed of molecules forming a definite structure, this structure, like the whole crystal, is subject to physical influences, and its component molecules are obedient to physical laws. So the molecules and groups of molecules forming the living protoplasmic structure are pulled down by gravitation. The molecules vibrate with lesser amplitude and draw together in cold, vibrating with greater amplitude and so tending to move apart when warmed. And as warmth makes molecular movements in any substance freer, so water makes possible still greater freedom of molecular movement in those substances which dissolve in it. There are substances, however, which neither repel water as do the fats and oils, nor go into solution in it as do many salts, but which still absorb water in great quantity. This absorption results in greater freedom of molecular and even of massive movement. Protoplasm is one of these substances; it swells as it absorbs water, and its circulation, as well as its molecular movements, becomes more rapid, up to the optimum. If still more water is forced into it, the molecules and groups of molecules composing it will be forced so far apart by the molecules of water enclosed, that the definite protoplasmic structure will be strained or destroyed, and the massive movements will accordingly change or cease.

Without going further into the subject now (see the next chapter), it may be stated that the growth of the living organism, like that of the crystal, is in accordance with the sensibility of its component molecules and groups of molecules to physical and chemical influences. The difference between the lifeless crystal and the living organism can be suggested—not definitely stated, however—in this way: the molecules of the crystal, and the crystal as a whole, are entirely subject to the prevailing balance of physical forces; the living organism, on the contrary, is able to modify, change, or maintain the balance of physical forces. When it ceases to be able to do this it dies, it becomes like the crystal. This power peculiar to living organisms, whatever it may be dependent upon, does not necessarily imply any greater sensitiveness to physical forces than would be representable by the sum of the sensibilities of all the substances composing and contained within the living organism (p. 185). But the organism is sensitive, and its growth corresponds to the forces or influences to which the organism is subjected quite as much as to the matter with which it is supplied.

What is growth? Of this no adequate definition can be given, although for each mind the word possesses a certain significance. Physiologists have always attempted to state in what growth consists, and have always failed. Our conception of growth should be clarified at once by distinguishing this phenomenon from the others ordinarily accompanying it. Growth is a part of the process of development. Growth and differentiation together accomplish development. Differentiation is that specialization in structure which follows and contributes to specialization in function. Differentiation is limited by the number of parts and of cells, in other words, by the size of the body. In a small body little differentiation is possible, in a large one much. But it does not follow from this that the largest bodies are the most highly differentiated in structure and function;

they are not yet, nor will they ever be unless differentiation keeps pace with growth. Does growth then consist in increase in size? A cell may elongate, but this will not necessarily be growth. We can easily imagine a cell being subjected to a pull which would elongate it, or to a pressure which would extend as well as compress it; or, indeed, within the cell itself a pressure resisted less in one direction than in others would cause the cell to elongate. In the last case there is stretching because of the pressure developed within the cell by its osmotically active contents. In the two preceding cases, the cell changes its dimensions because it is subjected to a force from outside itself which it cannot resist. In none of these cases has growth taken place. If, however, these changes in dimensions are made permanent by work done by the living cell itself in translocating and depositing insoluble material in such positions as to fix the new form or the new dimensions, growth will have taken place. Growth, the fixing of the new form or new dimensions, follows the change accomplished from without. But permanent change of form or of dimensions may be accomplished by forces wholly outside the plant; for example, by stretching the cell beyond the limit of elasticity of its walls. This would not constitute growth.

Growth, then, does not necessarily consist in an increase in volume, for there are evidently cases of unquestioned growth without this. The boy increasing in stature and the vine increasing in length, decreasing in breadth or thickness meanwhile, are growing though not increasing in volume. There is necessarily increase in volume of parts or organs, but not of the whole organism, in such cases of growth. On the other hand a rise in turgor which increases the volume of a part is not growth; this is merely expansion. Growth is a process dependent upon the formation of new protoplasm, and though it usually results in increase in volume, in increase in weight or mass, and in increase in substance, it is not essentially any of these.

Growth is made possible by cell-division, but it does not consist in the formation of new cells, for new cells can be formed by the mere division of old cells. Each cell, each kind of cell, and hence each organism, has a maximum which its size normally never exceeds. Cells which have attained their maximum size can continue to contribute to the growth of an organ only after doing what will make possible the formation of new protoplasm. Cell-division, a process of rejuvenation, accomplishes this. The smaller daughter cells, each with its own nucleus instead of with only a share of the single nucleus of the undivided cell, are more vigorous than the mother-cell at maturity; they form new protoplasm as well as other products from the food furnished them; and they then increase in size. In a meristematic tissue, such as that at the tip of the stem or root or in the cambium, we have the first and the *fundamental* stage in the process of growth, namely, the formation of new protoplasm and of new cells. Behind the tip of stem and root, and on either side of the cambium, we have the later, the *evident* stage, when increase in size or volume, in mass and in substance, takes place.

Evident growth takes place when the body or any part of it permanently increases in volume or in size. Increase in substance, which results in increase in weight, may take place after all growth has ceased. It may be merely the storing up of food elaborated at one time to be used later, or it may be the absorption of water. This last, however, invariably results in the increase in volume of the parts, or in the increase in turgor, or both at once. Any absorption of water by dry animal and vegetable substances is followed immediately by swelling—a phenomenon from which hypotheses regarding the minute structure of organized bodies have been more or less successfully deduced. Beyond the point at which swelling by the intussusception of molecules of water between the molecules or groups of molecules of the formed substances would cease, increase in volume may still go, by reason of the structure and composition of cells. The presence of osmotically active substances in cells which can absorb water ensures increase in pressure within the cells, and this pressure will distend the enclosing protoplasmic and cellulose or other walls. Up to a certain point, easily conceived but not easily determined, the increase in volume due to the absorption of water is genuine growth, and the second stage in growth, the one which I have designated as *evident* growth, consists mainly if not wholly in the absorption of water. But as the water-content of any cell or tissue or organ is subject to fluctuation, and as the turgor and, consequently, the volume also fluctuate with the water-content, it is difficult to tell when growth ceases and turgor-swelling begins. Both are vital processes in the sense that they depend upon the physical and chemical conditions established by the living protoplasm, but they are distinct processes, fluctuations in size due to changes in turgor taking place even long after true growth has ceased to be possible (see pp. 167, 168). Whether growth depends upon turgor or *vice versa* is still to be conclusively shown by experiment.

That evident growth consists mainly in the increase of the water-content of the growing part has long been known to be the case in plants, though only recently properly emphasized for animals.* A longitudinal section through the tip of a growing stem or root, or a cross-section through the stem of a dicotyledonous plant during its period of growth in diameter, will show at least three distinguishable regions. These are indicated in the accompanying figures (pp. 168, 169) of a longitudinally sectioned root of *Azolla*. In the diagramatic Figure 7 the three regions of cell-formation (1), cell-growth (2), and cell-differentiation (3), are indicated. These are shown in detail in the figures 8, 9, 10. Figure 8 (corresponding to 1 in 7) represents the tip of the root with its cap (*Cap*), dermatogen and epidermis (*Ep.*), cortex (*Cor.*), and central cylinder (*c. c.*), all of which come directly or indirectly from the division of the large apical cell. The meristematic and embryonic cells are full of dense protoplasm. Figure 9, taken from further up in the same root, corresponds to region 2 in figure 7, and shows that the increase in size of the cells of the different layers is accompanied by a great increase in the volume of the cell-sap, which accumulates in large vacuoles, without there being any considerable increase in the amount of protoplasm in each cell. Figure 10 corresponds to region 3 of figure 7, and shows how the cells change in taking on their definitive characters, *Ves.* indicating some of the changes taking place during the formation of a vessel in the central vascular bundle. In this region the amount of protoplasm decreases not only proportionally but absolutely. There can be little more if any permanent increase in volume in this region, although there may be increase as well as decrease in volume because of differences in turgor solely.

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* Davenport, C. B. The rôle of water in growth. Proc. Boston Soc. Nat. History, vol. 28, 1897. Experimental Morphology, Part II., 1899, and the literature there cited.

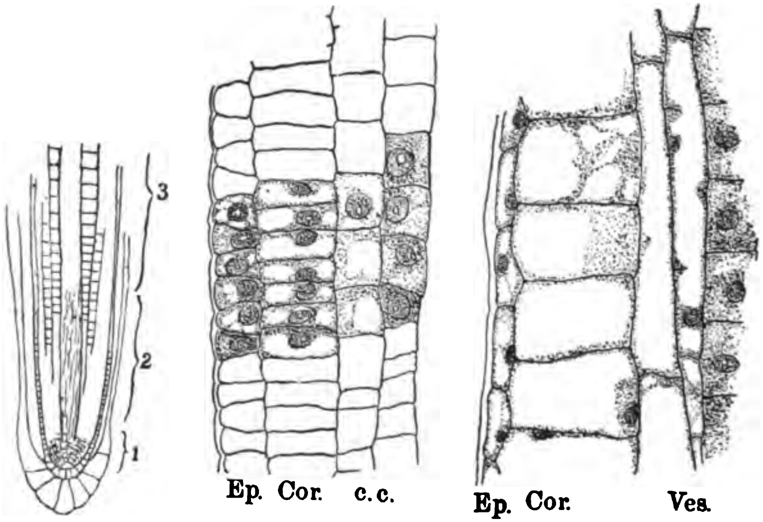

FIG. 7. FIG. 9. FIG. 10.

Figures 7—10. Longitudinal sections of *Azolla* root. Fig. 7—diagramatic—showing region of cell-formation (1). cell-growth (2). cell-differentiation (3). Fig. 9.=2 in Fig. 7 more highly magnified. Fig. 10.=3 in Fig. 7 more highly magnified.

The factors contributing to make growth possible may be grouped under three heads: 1st, there must be an adequate supply of material; 2d, there must be an adequate amount of room; 3d, there must be the impulse. Physiologists are not able to reduce to definite physical and chemical terms what is comprehended under this last head, and it has still to be ascertained whether the necessary impulse comes from within or from without, whether it is inherited or is new. But without the impulse there will be no growth.

Growth will not be possible without the needed materials and space. The substances essential for growth are those essential for life, but they may be grouped into two categories—nutritious substances, and otherwise useful substances. The nutritious substances furnish the materials of which the protoplasmic structure and the cell-wall are built, and those compounds which in respiration yield the energy needed by the part to complete the first stage of growth.

If the supply of food is constantly sufficient during the period of growth, both construction and enlargement will be uniform, other things being equal; but if the supply varies in amount, the rate of growth will vary correspondingly. It is found, for example, that the growth of green and independent plants is periodic in a much more marked degree than that of plants which obtain their food ready-made. During the day, while food is being made and accumulated in the organs photosynthetically active,

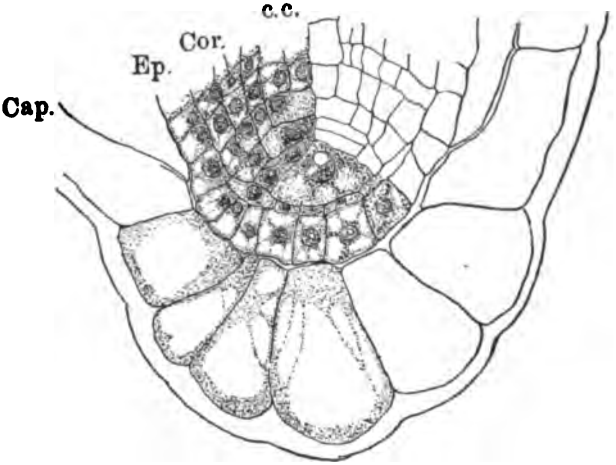

FIG. 8.

Figure 8. Tip of root of *Azolla* showing apical cell and region of cell-formation=1 in Fig. 7 more highly magnified.

growth is slower than during the night, when food is supplied in abundance to the growing parts.* This periodicity is far less marked in seedlings, with an abundant food-supply in the cotyledons or in the endosperm, and in young plants growing up from bulbs, tubers, and other parts in which food is stored. The growth of parasites and saprophytes may also vary periodically if they are subjected to periodically varying conditions. Light affects growth quantitatively, as well as directing it in the ways to be described in the next chapter (p. 208 *et seq.*). If plants furnished with a constant food-supply are subjected to otherwise constant conditions, their growth rate will be constant for a time. For reasons not wholly understood, but certainly including other factors than food-supply, the growth-rate of any part or organism will rise to a maximum and afterward fall again. For each cell and for each individual there is what has been rather pompously termed "the grand period of growth." This means simply that from its formation by the division of its mother-cell until the time when it ceases to increase in volume, each cell passes through a period during which it can grow, and during which its rate of growth gradually rises from nothing and falls again to nothing. After growth ceases, differentiation may still go on as a separate process. The maximum growth-rate is not necessarily coincident with the maximum food-supply or with the maximum of any other tangible factor.

Sachs and other physiologists† have called attention to the fact, without fully explaining it, that the growth-rate does not steadily rise and fall to and from the maximum, but that there are "discontinuous" (*stossweise*) variations apparently quite independent of the environment of the organism. It may be suggested that our analysis of growth, according to which it consists in two distinct stages—the one *fundamental*, in which new protoplasm is formed, the other *evident*, in which the cells expand—may suggest a partial explanation. Without a sufficient number of new cells, and without a sufficient amount of new protoplasm, no expansion can take place. Unless the two processes keep pace with each other, the mensurable one will necessarily be irregular.

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* Sachs, J. von. Physiology of Plants. Oxford, 1887. Miss Gardner (Trans. and Proceed.. Bot. Soc. Pennsylvania. Vol. I, No. 2, 1901) claims that the growth of roots is faster by day than by night. This reresult is probably due to the favorable action of light on processes upon which growth depends rather than upon growth itself. The question deserves critical investigation.

† Sachs, J. von. Über den Einfluss der Lufttemperatur und des Tageslichts auf die stündlichen und täglichen Änderungen des Längenwachsthums (Streckung) der Internodien. Arbeiten des bot. Instituts Würzburg, Bd. II., 1872. Gesammelte Abhandlungen, Bd. II. Lectures on the Physiology of Plants, English transl., p. 552. Kraus, Gregor. Physiologisches aus den Tropen, I. Annales du Jardin Botanique de Buitenzorg, vol. XII., 1895.

In this connection the fact already referred to (pp. 167, 168), that changes in volume may take place quite independently of growth and because of turgor changes only, may be considered in somewhat more definite fashion. Kraus* pointed out long ago, and has confirmed his observations made in Europe by others in the tropics, that there are daily variations in the length and thickness of stems and branches, leaves, buds, and fruits. "The diameter of a tree-trunk, for instance, increases measurably till the early morning hours; it then decreases till nightfall, when it begins to increase again." This is due to the variation in volume of the cortical and other parenchyma cells caused by the difference in the rate of transpiration at different hours of the day. Absorption by the root-hairs continuing at a rate much more uniform than that of transpiration—at night slightly higher, by day slightly lower—the turgor and the volume of all living and sufficiently thin-walled cells will vary accordingly. This variation, wholly independent of all vital functions, except those which govern the composition of the cell-sap and the permeability of the protoplasm, continues in organs no longer growing, but may also, during growth, contribute to the irregularities in the curve of growth.

The otherwise useful substances referred to above (p. 169) are mainly water and certain salts not directly entering into the construction of living protoplasm. Some of the water forms an integral part of the protoplasmic structure (pp. 6–8), but the greater part of it serves as the vehicle of nutritious substances brought to the cell, and as the solvent of all the soluble substances in the cell. As the essential and invariable ingredient of cell-sap, it is the material which maintains the second or evident stage of growth. The volume of the cell depends upon the water and upon the compounds dissolved in it. The composition of the cell-sap is regulated by the living protoplasm which adds to or takes from it soluble compounds of diverse sorts,—assimilable and excreted matters, such as the sugars and organic acids respectively. Besides these, it is claimed that the cell owes its turgescence to certain soil-constituents, especially the salts of potassium. According to Copeland,* the degree of turgescence in ordinary roots, stems, and leaves is only slightly dependent upon food-manufacture, and is mainly due to a substance or to substances which cannot be used to keep the plant from starving. Copeland concludes from his experiments on the effects of light and darkness, heat and cold, that the rate of growth has much more effect upon the turgor of the growing part than *vice versa*.

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* **Kraus, Gregor.** *l. c.* **II,** *and earlier in* **Die Wasservertheilung in der Pflanze, 1881,** *and* **Die Gewebespannung des Stammes und ihre Folgen. Botanische Zeitung. 1867.**

The fundamental stage of growth, consisting in the formation of new protoplasm, implies the intussusception or interpolation of new particles between the older parts of the structure, or the application or apposition of new particles upon the older, or both of these processes. In either some force must be exerted. If the cell is distended while the new particles are being formed and placed, the introduction of new particles between the older will be proportionally easier. So the turgescence of the cell, tending to keep all parts stretched, may contribute to such growth. But Copeland had in mind evident growth, increase in volume, rather than the formation of new protoplasm. The turgor of the cell may be sufficient to stretch it, to increase its volume, but this does not necessarily mean growth, as we have already seen; and again, if the cell is stretched, if its volume is increased, by other means, its turgor must either keep pace with this increase in volume, or fall. If it keeps pace, because of the composition of the cell-sap and of the abundance of water to be absorbed, it will be impossible to determine whether evident growth is dependent upon turgor and is regulated by it, or not. If the turgor fall during the increase in volume, it must be shown that this fall is due to no other cause. On this point decisive experimental evidence is still wanting.

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* **Copeland, E. B. Über den Einfluss von Licht und Temperatur auf den Turgor. Inaug. Diss., Halle, 1896.**

From experiments by True* on the different rates of elongation in the roots of seedlings grown in water-culture and suddenly transferred to culture media of higher or lower density, it would appear "that growth and turgor-pressure here stand in no directly proportional relation to each other." Furthermore, Pfeffer† has shown, in a case where turgor would be at least equally helpful, namely, in the formation of cell-wall, that it is not necessary. The question resolves itself then into this: is turgor-pressure,—so useful and so necessary in maintaining the form of cells, tissues, organs, and organisms—the force by which increase in volume is attained, or only the means by which increased volume is maintained? Apparently the latter is more likely to be the case; but if this is true, what is the force by which the living protoplasm expands, and by which it stretches its bounding walls? If turgor is not the force by which visible growth is accomplished, then the increase in the amount of water and in the volume of cell-sap in the growing part is only the evidence, not the intrinsic quality, of visible growth. After all, we are forced to confess that the physiologist's knowledge of the forces by which the living protoplasm works is very incomplete.

Room is needed. Without it growth cannot take place.

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* **True, R. H. On the influence of sudden changes of turgor and of temperature on growth. Annals of Botany, vol. 9, 1895.**

† **Pfeffer. W. Druck und Arbeitsleistung durch wachsende Pflanzen. Abhandlungen d. K. Sächs. Gesellsch. f. Wissensch., Bd. XX., Heft 3, p. 429, 1893.**

Cell-division may take place even where there is not enough room for growth, but it does not constitute an essential part of the process of growth, though it usually precedes growth and makes it possible. An organ consisting of two hundred cells has not grown in any sense when these cells by mere division have become four hundred. Under normal conditions, however, growth will follow, increase in volume and in amount of protoplasm taking place when there is enough room.*

Growing parts exert, or may exert, great mechanical force. Illustrations of the truth of this assertion may be observed almost daily.† Until recently, however, the attempts to determine the amount of force which a growing part can exert have yielded only inadequate results. It is necessary to employ such apparatus that all the force developed by the growing plant will be exerted directly upon the recording instrument. The best instrument so far devised is Pfeffer's.‡

Pfeffer's description of his apparatus will explain the accompanying illustration, reduced from the original figure. "The spring is supported on an iron bar (*d*) 14 mm. thick which is rigidly attached by means of double screw clamps (*e*) to the upright posts (*ss*) of the stand. The measuring spring (*f*) can be changed, for the plate (*l*) which carries it is fastened by the screws (*kk*) to the solid brass plate (*g*). By raising or lowering this plate the spring can be moved up or down, to or from the plaster-of-Paris block (*a*). For this purpose the plate (*g*) rests upon three screws (*h*) which pass through correspondingly threaded holes in the flattened and expanded part of the bar (*d*). Upon the metal plate on the upper side of the spring is fastened the glass plate (*c*) by means of a small amount of plaster of Paris. The upper needle is fastened within the spring by means of shellac, while the lower one is adjustable by means of the screw (*i*). The flower-pot (*n*) containing the root set as in the figure in plaster of Paris is firmly pressed into the iron ring (*m*) fastened by two screws to the upright (*s*). The small plaster block (*b*) is now fitted to the root-tip and fastened by plaster of Paris to the glass plate (*c*) so that the root-tip is over the middle of the spring. The screws (*h*) are now turned up so that the two plaster blocks (*a* and *b*) are pressed lightly together. The saw-dust in the pot should be kept moist. The plaster blocks may be constantly moistened by wrapping them with filter-paper wet through a strip of paper connecting with a reservoir. The horizontal rod (*o*) pressed down on the pot (*n*) and

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* On the effects of mechanical restraint on the growth and other behavior of plant-cells and parts, consult Newcombe, F. C. Influence of mechanical resistance on the development and life-period of cells. Botanical Gazette, vol. 19, 1894. Pfeffer, W. Druck und Arbeitsleistung durch wachsende Pflanzen. Abhandlungen d. K. Sächs. Gesellsch. f. Wissensch., Bd. XX., 1893. *Also* p. 187 of this book.

† For striking observations under this topic see Kerner and Oliver's Natural History of Plants. Vol. I. part 2, pp. 513-17.

‡ Pfeffer, W. Druck und Arbeitsleistung.

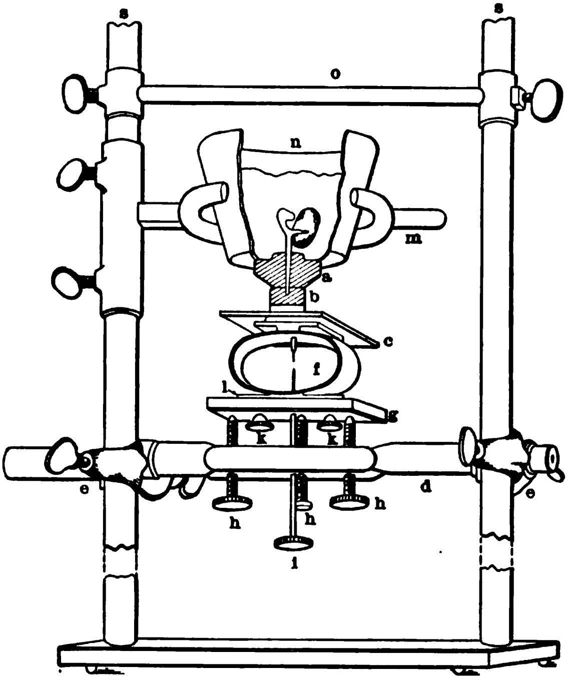

FIG. 11.

Figure 11. Pfeffer's apparatus for measuring the force exerted by growing roots or stems. (Reduced from the original figure.)

fastened by screws to the uprights (*ss*) holds it securely in the ring." By appropriate modifications of this apparatus, growth in diameter as well as in length can be investigated, in stems as well as in roots.

The following table indicates the effective pressures developed by growing roots:

LONGITUDINAL PRESSURE

NAME OF PLANT.	PRESSURE PER SQ. MM.	PRESSURE IN ATMOSPHERES.
Faba vulgaris	98 + grams	9.5
Zea mais	138 + "	12.4
Vicia sativa	111 + "	10.7
Aesculus hippocastanum	68 + "	6.6
		Mean = 9.8

TRANSVERSE PRESSURE

Faba vulgaris	44 +	4.3
Zea mais	68 +	6.5

These figures, obtained by averaging those in Tables I and II of Pfeffer's paper, indicate that although the growing parts are composed of such soft materials, they are capable of developing under resistance a force which makes continued growth possible under all ordinary conditions. Cross and longitudinal pressures developed by stems are probably equal to those developed by roots, but the evident difficulties in the way of measurements as exact as those for roots cause the figures reported by Pfeffer to be somewhat lower, as for example, 5.8 and 5.5 atmospheres for the longitudinal and cross pressures developed by the stems of seedlings of *Faba vulgaris*.

The growth of plants and animals is as a rule so slow that accurate measurements are difficult to obtain. Besides this, their behavior in other ways is very likely to complicate any attempt to determine either the amount or the rate of growth. The almost constant movement of plant-parts out of doors under the influences of wind, sunlight, warmth, etc., and the constant spontaneous movements called circumnutation, make it seem absolutely necessary to experiment upon small plants indoors; but when this is done, other complications ensue, such as are due to watering the soil and its subsequent drying, the jarring of the measuring instruments, etc., etc. Furthermore, not all plants grow in straight lines. The tips of the stems of many are sooner or later so curved that the length of these parts can only be estimated. To overcome these various difficulties many instruments have been devised. From the direct observation and measurement of small organisms or parts by means of microscopes, vertical or horizontal, to the complicated self-recording auxanometers of the well-equipped physiological laboratory, the utmost variety in methods and means exists. Illustrated descriptions of instruments are so accessible that space need not be taken here for them.[*] Most of these instruments are but modifications and improvements of those invented by the masters in plant-physiology, especially by Sachs. The principle of all is to magnify the growth so that the evidence or the record of it is visible. The need of this is made evident by the following figures—

Observer.	Plant.	Part.	Growth per minute.	% of growth per minute.
True[†]	Vicia Faba	roots growing in water	0.012 mm.	
Kraus[‡]	Bambusa sp?	stalk	0.040 mm.	
Askenasy[§]	Triticum sp?	stamens	1.05 mm.	37.5
Hofmeister[¶]	Spirogyra	cell		7.5
Brefeld[††]	Coprinus stercorarius	stalk	0.225 mm.	

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[*] See Ganong, in Botanical Gazette, vol. XXVII., 1899.
Arthur, " " " " XXII., 1896.
Stone, " " " " XXII., 1896.
Golden, " " " " XIX., 1894.
Frost, " Minn. Bot. Studies, " XVII., 1894.

[†] True, R. H., *in* Annals of Botany, vol. IX., p. 371, 1895. Figures in Table I give this average.

[‡] Kraus, G., *in* Annales du Jardin Botanique de Buitenzorg, vol. XII., 1895.

[§] Askenasy, *in* Verhandl. d. naturh- med. Vereins in Heidelberg, 1879.

[*] Hofmeister, *in* Jahreshefte d. Vereins f. Vaterl. Naturkunde in Württemberg, 1874.

[††] Brefeld. Untersuchungen über Schimmelpilze. Heft 3, 1877.

These numbers, however, are much above the average, even the Bamboo being a notoriously rapid grower. The extraordinarily rapid growth of the stamens of wheat takes place when they are released from mechanical hindrance by the spreading apart of the scales.

Probably the average rate of growth for plants does not exceed, if it equals, 0.005 mm. per minute. Certainly there are many plants which grow so slowly that no one has had the patience and skill to make accurate measurements. The lichens are among such slow growers, though these must grow at different rates as is evident in the parts of California where the very large "lace-lichen" (*Ramalina reticulata*) and crustaceous and small foliose lichens live side by side.*

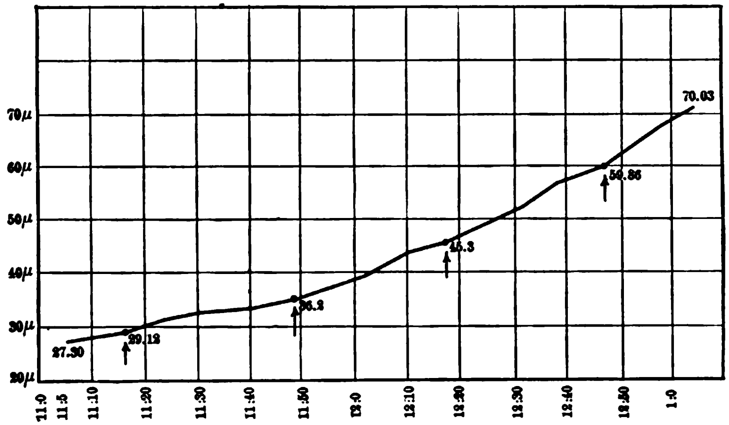

Figure 12. Curve of growth in part of a filament of *Bacillus ramosus.* (From Ward.)

In connection with these figures as to the rate and the percentage of growth of larger and in some cases "higher" plants, it may be of some interest to compare the curve of growth obtained by Marshall Ward† while studying bacteria. The accompanying diagram gives the curve of growth in part of a filament of *Bacillus ramosus*, 27.30 μ* long at the beginning, 70.03 μ long at the end of the period of observation, two hours. Cell-divisions occurred at the points indicated by the arrows. Between the first and the second cell-divisions there was an increase of 6.79 μ in length, between the second and third of 9.10 μ, between the third and fourth of 14.56 μ. Between the first and second cell-divisions there was a lapse of thirty-three minutes, between the second and third, twenty-six minutes, between the third and fourth, thirty-one minutes, an average of thirty minutes. The average growth during these three periods was 10.14 μ between each two divisions, or a growth of about one-third of a μ per minute. This would appear to be slow growth in comparison with that indicated by the table on page 177; but the growth of many-celled organisms represents the combined increase in length accomplished by a large number of comparatively large cells working together. Ward's bacillus is a unicellular organism of minute size. A moment's calculation will show that its average increase in length in every thirty minutes, that is, between each two cell-divisions, is 25%. This is certainly a much higher rate of growth than is possessed at any time by higher organisms,† and it is merely the average rate during a half-hour. Doubtless its maximum growth is decidedly higher. Probably the growth-rate of bacteria is higher under favorable conditions than that of any other group of organisms. Their high growth-rate, the rapidity with which they attain the size when cell-division is possible, the promptness with which they divide, the immediate growth of the daughter cells at a high rate, all contribute to the effectiveness of these minute organisms.

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* See Peirce. G. J. On the mode of dissemination and on the reticulations of *Ramalina reticulata.* Bot. Gazette, vol. XXV., 1898. Ditto. The nature of the association of alga and fungus in lichens. Proc. Cal. Acad. Sci.. Series III., Botany, vol. I.. 1899. Ditto. The relation of fungus and alga in lichens. American Naturalist. vol. XXXIV., 1900.

† Ward. H. M. On the biology of *Bacillus ramosus.* Proc. Roy. Society vol. LVIII.. 1895.

It was stated on page 166 that each cell, each kind of cell, and hence each organism, has a maximum which its size normally never exceeds. Let us seek a reason for this.

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* A μ or micron equals $\frac{1}{1000}$ millimetre.

† Since going to press, a review of Buechner's paper (Zuwachsgrössen und Wachsthumsgeschwindigkeiten bei Pflanzen. Dissertation, Leipzig, 1901) has appeared (Bot. Centralbl., Bd. 90, p. 500, 1902) in which the growth of the pollen-tube of *Impatiens Hawkeri* is reported at 220% and of branches of higher plants as 1% in a unit of time and length.

Each of the component cells of a multicellular tissue, organ, or organism, is limited in all its behavior by the cells which surround it. The single cell of the unicellular organism is not so limited, being constrained only by the conditions prevailing in itself and in its lifeless surroundings.

Attempts have been made to attribute the maximum size ordinarily attained by organisms to one or two of the three conditions named on page 168 as making growth possible. It is said that an organism or a cell cannot grow beyond a certain size because there may not be room. If this be true, then the word room must be used with a broader meaning than that attached to it in our discussion on pages 173 and 174: it must mean, as stated on page 6, freedom from interference of every sort. This last is undoubtedly true, for a plant with such an impulse to grow that it might otherwise cover the whole earth would be prevented by the presence, if not by the attacks, of the other organisms living at the same time. So the individual is kept within a certain size.

Again, it is said that nutrition fixes the limit of growth. In a growing spherical cell, the increase in surface and in mass are to each other as the square to the cube, "in other words, the smaller the cell, the greater is the surface in proportion to the mass; and the more the cell grows, the less does the surface grow in proportion to the mass."* It is said that since all food-materials are taken in through the surface, the supply of food will be insufficient when the surface becomes too small in proportion to the mass. This implies, however, that the absorbing power does not increase proportionally with the mass. The absorbing power, as we have seen, is the osmotic force exercised by the cell-sap upon the solutions and the constituents of the solutions outside the cell. This osmotic force depends upon the differences in the composition, absolute and proportional, of cell-sap and surrounding liquid. The larger the volume of cell-sap, the more slowly can it be made like the liquid outside, *i. e.* the more slowly will the osmotic force be diminished. We have no reason to think that the osmotic force is less, for the turgor is not lower in large than in small cells. So it cannot be merely the ratio of surface to mass which is the determining factor.

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* Verworn, M. Allgemeine Physiologie, Ite Aufl., p. 511. 1895. Engl. transl. by Lee, General Physiology, p. 530, 1899.

The high turgor and osmotic force maintained in large cells imply, besides the density of the cell-sap, that the enclosing membranes of the cells are not freely permeable. Upon the impermeability of the membranes and upon the composition of the cell-sap depend the turgescence, the plumpness, of cells of large size. The membranes must possess strength as well as impermeability, but it is their impermeability which makes it necessary that they should also be strong. It is this change in the *quality* of the surface rather than in the mere ratio of surface and mass, which is the important factor in limiting size. But this is not all.

Whatever may be the distinct functions of nucleus and cytoplasm, it is safe to conclude that neither can be greatly increased or diminished in amount or in activity without affecting the other and the cell as a whole. By chilling cultures of *Spirogyra* while in a state of cell-division, Gerassimow* regularly secured the formation of cells without nuclei, normal cells, and cells with double the usual amount of nuclear substance. He found that the non-nucleated cells grew very slightly in length, that normal cells grew normally, that cells with more than the normal amount of nuclear substance attained a larger size and divided later than normal cells. Since the volume of the nucleus does not keep pace with the volume of the cytoplasm or of the cell as they both increase shortly after the cell is formed by division, the disparity in the amounts of nuclear and cytoplasmic substances increases. It is conceivable that growth ceases when the amount of cytoplasmic in proportion to nuclear substance has attained the optimum or maximum; in other words, that the limit of growth is fixed in the first and fundamental stage, the subsequent increase in size going only to the limit set by the amount of protoplasm formed.

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* Gerassimow. J. J. Über den Einfluss des Kerns auf das Wachsthum der Zelle. Moskau. 1901.

If the nucleus were larger and the cytoplasm proportionally abundant, if the permeability of the enveloping membranes and their tensile strength were proportionally increased, if the absorbent power (osmotic force) of the cell were also raised proportionally, is there any reason why the cell, the organ, and the organism should not grow larger? The question cannot be answered. Many organisms do not attain larger size when, so far as we can now see, it would be possible for them to do so. Are the bacteria so small because they have so little nuclear substance in proportion to cytoplasmic? On the contrary some authors* have claimed, from the behavior of bacterial cells toward staining agents, that they are mainly nuclear substance with but a thin layer of enveloping cytoplasm. The amount of room and of food which the individual bacteria could occupy and consume would certainly suggest that they might attain larger size. Their enveloping membranes appear to be sufficiently permeable and strong for larger organisms. Yet the bacteria remain minute, and no reasons now known can account for their size. If our mechanical explanations fail on these organisms, are they any more certain to be correct when applied to the growth of larger ones? What limits the size must have to do with the sensitiveness, the irritability, of the living matter, and this leads us to the subject of the next chapter.

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* See in Migula's System der Bakterien. Bd. I., pp. 72-80, the discussion of this point and the references *pro* and *con*.

CHAPTER VI

IRRITABILITY

The preceding chapters have taught us that living organisms are composed of chemical compounds and that they work by physical force. The body of a living plant consists of living protoplasm and of lifeless substances. The functions of a living plant consist in chemical changes some of which liberate energy, or store it, while others result in the accumulation of matter, lifeless and living. These functions are carried on by the living organism, they do not simply take place; but the organism lives and carries on these functions only by using chemical compounds and physical forces. Just as chemical and physical processes are affected by prevailing conditions, so the living organism is affected by each factor of its environment. When the factors change, the organism is differently affected, just as, with changing conditions, ordinary chemical and physical processes also change correspondingly. As there is an optimum condition, which consists in temperature, illumination, supply of water and of other substances, etc., for each chemical reaction taking place in the laboratory and in nature, so there is an optimum condition for that complex of chemical reactions constantly taking place in the actively living organism. Any departure from the optimum modifies some or all of the chemical changes in the organism so that there is a different and less favorable balance in the complex. Conversely, any approach to the optimum condition so modifies some or all of the chemical changes that their balance is more favorable. When we conceive a living organism, even the simplest and smallest, as being a definite structure (protoplasm) consisting of simple water molecules and of other molecules highly complex and therefore comparatively destructible, built together and enclosing many other compounds, simple or complex, we have the ground-work for a rational conception of the sensitiveness of living organisms to their surroundings, that is, of their irritability.

A solid mass of the metals and jewels ordinarily employed in the construction of a chronometer may be subjected to much harsher treatment without danger of destruction than the same weight of the same substances arranged as a chronometer. Though the substances are the same, their arrangement in the two cases is the reason for their sensitiveness, or their power of resisting violence. Living substance, protoplasm, is a structure infinitely finer and hence moré delicate than a chronometer. Furthermore, protoplasm is composed of many more chemical compounds than those entering into the structure of a chronometer. The molecules of each of these compounds are composed of so many atoms of so many different elements that they are far less coherent and stable than the simple one, or two, or three atomed molecules forming the substances in a chronometer. Besides all this, these large numbers of atoms are combined into molecules, these complex molecules are arranged in groups, these groups enclose and are surrounded by water, and the water holds in solution oxygen and a variety of compounds. The component atoms of these compounds have affinities for other atoms as well as for those with which they are combined. Furthermore, the substances may not all be in the molecular state in the solution; the component atoms of some substances may be more or less completely dissociated.* In this condition they will be still more susceptible to physical and chemical influences than if combined into molecules, and they will affect the protoplasm with correspondingly greater promptness. The intimate contact of the aqueous solution, the cell-sap, with the living protoplasm, and the complete distribution of the solution throughout the cell, insure the thoroughness with which the protoplasm will be affected. The complexity of protoplasm in composition and structure, and the physical and chemical properties of the cell-sap which is everywhere within it, help us to see that protoplasm is necessarily as well as actually the most unstable and the most complex, structure known.

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*See Ostwald, W. Outlines of general chemistry, Eng. transl. by Walker, London and New York, 1895. Nernst, W. Theoretical chemistry, Eng. transl. by Palmer, London and New York, 1895. Jones, H. C. The theory of electrolytic dissociation and some of its applications. New York, 1900.

Comprehending these facts, we see reasons for the sensitiveness of protoplasm to outside influences. But lifeless protoplasm—imagining such a thing for the moment—although it possesses all this complexity of structure and of composition, and is therefore sensitive to influences from without, is not the seat of the physiological processes, of the destructive and constructive chemical changes, which are constantly going on in living protoplasm. Indeed the dry seed is far less sensitive, as we have already seen (pp. 9, 10), than the same seed after water has been absorbed and germination has begun. Wherever there is actively living protoplasm, *i.e.* a complex structure among the compounds of which and within which chemical changes are constantly taking place, we have the conditions for irritability: the more complex the structure and its component and enclosed compounds, or the more varied and the more rapid the chemical changes taking place in the structure, the greater will be its sensitiveness to external influences. The higher the organism, the more complex is its structure, the more varied or the more rapid are the chemical changes taking place in it, and therefore it is the more sensitive. The organism is dormant, unsensitive, unirritable, when its physiological processes are slow or simple; the organism is dead when its physiological chemical changes cease and its structure breaks down. Its component molecules may still be there intact after the organism ceases to live, but their arrangement is changed, the sensitiveness of the whole structure and of all its parts is diminished in proportion as the arrangement of the molecules is modified.

The irritability, then, of living organisms consists in a sensitiveness to external conditions which is due to the complexity in structure and in composition of the organisms themselves. To put this in more definite terms we may say that the irritability (which we may represent as x) of a cell, an organ, or an organism, consists in the sum of these factors, viz.—

(a) the sensitiveness of the component atoms of complex molecules to other forces and affinities as well as to the affinities which hold them together in these compounds.

(b) the instability of the groups of molecules.

(c) the instability of the protoplasmic structure which consists of water and these complex molecules.

(d) the number, variety, and speed of the chemical changes taking place in this structure.

(e) the number, variety, and speed of the chemical changes taking place between its component molecules and others enclosed among them or outside.

(f) the number, kinds, and degree of dissociation, of the atoms and molecules of the substances dissolved in the water in the cell.

Thus $x = a + b + c + d + e + f$, a sum greater than is attained in any known combination except the living cell.

Let us pass on now from these general considerations as a starting-point, to examine certain phases of irritability: *first*, the relations of irritability to the amount, kind, etc., of growth; *second*, the direction of growth, and movement, as depending upon irritability; *third*, the growth movements not evidently connected with irritability.

IRRITABILITY AND THE AMOUNT AND KIND OF GROWTH

Every actively growing organism must have, besides an adequate supply of material, an adequate amount of room, and the impulse to grow (see p. 168), at least the power to direct its growth according to its environment. This power is dependent upon the irritability of the organism and of its separate organs, their sensitiveness to forces and influences wholly external. Since the material of which it is composed came into existence, every organism has been subjected to external influences, some momentary or unequal, some persistent and uniform. The effects of these influences are more or less enduring, like the influences themselves, but presumably are far from permanent at the utmost. While the effect of one influence still persists, other influences are operating on the organism. The status of the organism at any one time represents the results of all the influences to which it has been subjected up to that time; its form, size, position, etc., are its response to all these influences. The condition of the organism and the influences bearing upon it, together determine how it will grow. The study of irritability at any one time, therefore, necessarily includes the results of irritability at other times earlier in the life of the individual.

We may begin our study with those mechanical influences to which plants are or may be subjected. When a growing part is enclosed within a bandage of plaster of Paris, two results follow, one of which has already been mentioned (p. 174).* The other we may consider now. The part not only lacks room to grow, but the plaster ligature relieves the enclosed part, as it does a broken arm or leg, of mechanical strain of nearly every sort. The tissues primarily contributing to the mechanical strength of the growing organ attain within the ligature neither such size nor such strength as ordinarily.† From this we may conclude that the mechanical strength of a part depends upon the strain to which it is subjected. This conclusion, reached from experiments in which the mechanical strain was reduced as much as possible, is enforced by experiments of the opposite sort, in which the mechanical strain was increased.‡ The strain consisted in traction, effected by means of weights

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*Newcomb, F. C. The influence of mechanical resistance on the development and life-period of cells. Botan. Gazette, vol. 19, 1894. Regulatory formation of mechanical tissue. *Ibid.* vol. 20, 1895.

† Pfeffer, W. Druck und Arbeitsleistung. Abh. d. K. Sächs. Gesellsch. f. Wissensch., Bd. XX., 1893. Also Pflanzenphysiologie, 2te Aufl., II., pp. 144-7, 1901.

‡ Hegler, R. Einfluss des mechanischen Zugs auf das Wachsthum der Pflanze. Cohn's Beiträge zur Biologie der Pflanzen, Bd. VI., 1893. Older literature here cited. *See also* Pfeffer, W. Besprechung Hegler's Untersuchungen. Berichte d. K. Sächs. Gesellsch. f. Wissensch., Sitzung vom 7ten Dec., 1891. *Also* Pflanzenphysiologie II., § 36. Derschau, M. von. Einfluss von Kontakt und Zug auf rankende Blattstiele. Inaug.-Diss., Leipzig, 1893.

suspended from threads passing over pulleys and fastened to growing parts. The following figures will illustrate the results obtained—

WEIGHT.	SEEDLINGS.		PETIOLES.
	Helianthus.	Phaseolus.	Heleborus.
Enough to break,	160 gr.	180 gr.	400 gr.
Used to strengthen.	150 "	165 "	
" " test on 2d day,	250 "		
" " " " 3d "	300 "		
" " " after several days,	400 "		
" " " on 7th day,		650 "	
" " " " 5th "			8⅓ K.

Subjecting otherwise weak stems to pull induces them to form strengthening tissues which would not ordinarily develop at all. Stems thus acted upon decrease their growth in length in proportion as they are stimulated to grow in thickness. Even a strain too slight to produce any stretching will have this effect.

The formation of strengthening tissues is proportional to the need. This is shown each year by fruiting plants. The fertilization of the egg-cells in the ovules of flowering plants leads to the production of seeds, the growth of fruit, and the considerable increase in weight of these and of the adjacent parts. The development of the fruit and its contents demands a corresponding growth both of conducting and also of mechanically strengthening tissues extending into regions quite distant from the fruit as well as in those near it.* A similar response to mechanical strain is shown by many mosses and liverworts. The stalks bearing the fruits grow greatly in length for a time. Later, when the fruits increase in weight, the stalks cease to elongate and become much thicker and stronger.

Plants are everywhere in nature exposed to mechanical strains of more or less force and constancy. The winds, flowing water, tides, waves, and the movements of animals apply mechanical force to living plants, and to these influences they respond by the increased or modified activity of the living protoplasm.

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*Pieters. A. J. Influence of fruit-bearing on the development of mechanical tissue in some fruit trees. Annals of Botany. X. 1896.

The most evident effects of winds are those deformities which usually, however, are more the result of injury than of stimulus. Trees in exposed places are unsymmetrical, their limbs short and broken on the side toward the strong or violent prevailing wind, while on the other side the limbs look as if they had been drawn along with the wind. But the root-system of such trees shows the stimulating effect of the wind without the deformities exhibited in the branches, the roots being longer and stronger on the windward than on the leeward side, the greatest strength developing where there is the greatest mechanical force to be resisted.

The ordinary swaying of stems and branches, and even of leaves on their stalks, acts as a stimulus to the living cells of a plant. The difference in the amounts of mechanical tissue in plants which carry their own weight and in those which lean, twine, and otherwise climb, is partly due to the difference in mechanical stimulus to form strengthening tissues. By tying an erect plant so firmly to a support that it cannot sway in the wind, or by supporting its weight on a frame, the plant will be deprived of those movements, stresses, and strains which normally stimulate it to develop strength.

Water-currents exercise similar effects to those of wind-currents, whenever they are rapid enough to develop any considerable force. Even slow water-currents have been found to stimulate and direct growth and movement in rather peculiar fashion. Thus the roots of certain plants, if suspended in clean running water, will bend so that the tips point and grow up stream. This phenomenon is known as *rheotropism.** The plasmodia of certain Myxomycetes will grow on a vertical strip of filter-paper always in the direction opposite to that of the current of water which is supplied to them, whether this be upward or downward. This phenomenon is called *rheotaxis*,* but it is not certain that it is not a response to obscure chemical stimuli rather than to a current of water merely. Rheotaxis and rheotropism are therefore probably distinct phenomena. The significance of rheotropism is not understood.

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* Juel, H. O. Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. f. wiss. Bot., Bd. 34, 1900. Newcombe, F. C. Rheotropism of roots. Bot. Gazette vol. 33 1902.

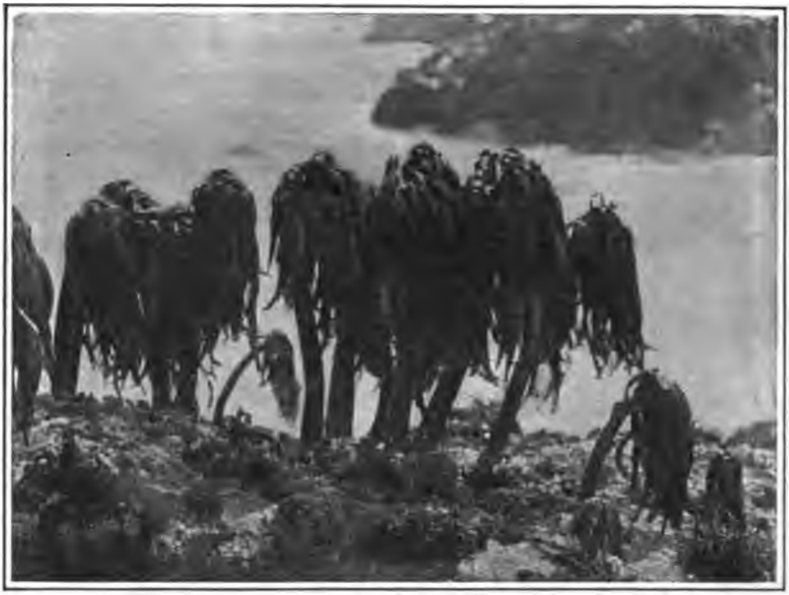

FIG. 13.

Figure 13. ***Postelsia Palmæformis.*** **Sea-palms at Point Lobos, near Monterey, California. Height about 2 feet. Photograph by Dr. W. A. Shaw.**

Waves and tides have not been studied experimentally in their mechanical relation to plants. It may be inferred, perhaps, that they produce movements which stimulate the plants exposed. Certainly plants which are to withstand the pounding of the waves must grow proportionally resistant. Is this simply a case of the survival of the accidentally toughest and fittest, or do tide and surf plants irritably react to the rude stimuli to which they are subjected? Of these buffetted forms the Sea Palms (*Postelsia palmæformis*) of the Pacific Coast are the most striking. Living between the tide-marks, always in the most exposed positions, these upright plants hold on and grow in spite of the tremendous pounding to which they are almost continually exposed. In toughness, strength, and elasticity their upper parts are equalled only by the closeness of the attachment and the strength of the hold-fasts. The accompanying figure suggests how rough their habitat may be in a storm.

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* Stahl. E. Zur Biologie der Myxomyceten. Bot. Zeitung, 1884.

From the foregoing we may conclude that a certain amount both of freedom to move and also of actual agitation is good for plants. This is exercise, apparently as desirable for plants as for animals, and presumably for the same reasons. It facilitates the transfer of nutrient substances and it stimulates the living protoplasm. Which factor is the more important it remains for experiment to determine.

In trees and shrubs the mechanical tissues are found especially in the wood. Where the seasons are sharply contrasted, as over the greater part of the temperate zones, the wood presents the familiar appearance known as annual rings. In mechanical strength the different parts of the wood vary considerably, the so-called "spring-wood," because of the larger size of the cells and the comparative thinness of their walls, being decidedly weaker than the thicker-walled, more compact, and often more abundant "autumn wood." It is through the wood, especially the ducts and tracheids, that the transfer of food-materials from roots to leaves takes place (see pp. 119-124). The wood is, therefore, both a mechanical and a vascular tissue. The one function or the other predominates at different times during the growing season and affects the growing and developing tissues accordingly.

Where growth is always possible and is practically continuous, annual rings are not formed. It is only where growth is periodic because of changing seasons, like winter and summer, dry and rainy seasons, that there are decided differences in the character of the wood. Certain other phenomena almost or quite coincide with the formation of annual rings. "Spring wood" forms (see p. 123) when sap-pressure is greatest, when the buds open and the leaves expand, when there is a sudden extension of the surface from which water will evaporate. At this time water must be abundantly supplied to the parts just emerged from the bud so that the new cells may expand to their proper size; food must be furnished these growing parts so that new cells and new protoplasm may form and the parts may continue to increase in size. When the buds unfold there is an immediate and great demand upon the conducting tissues, but as the parts increase in size and weight, the mechanical strength of branchlets, branches, and stem must increase also. With an increasing weight each spring and early summer there is an annually increasing mechanical strain upon the tree or shrub. This increased strain is yearly met by increased strength, and this is contributed largely by the "autumn wood."

The time during which the cambium cells give rise by division to new cells differentiating into wood and bast elements is much briefer than the season during which growth is apparently possible. According to Jost,* the greater part of the increase in thickness of stems and branches takes place in May and June (in Germany). This indicates that the activity of the cambium cells and of their immediate derivatives is controlled by influences outside of themselves. These influences are doubtless many, but we may distinguish some of them at least.

The young parts growing and developing from opening buds in the spring need much food and water, and they certainly transpire greater or less quantities of water-vapor. There is at this time an especially great and a fairly steady demand upon the conducting tissues for both food and water, not so much for transpiration, perhaps, as for growth in the full sense of the word; for food so that new protoplasm may be formed, for water so that it may properly expand. This demand would make itself felt first in the parts nearest opening buds. It is here that the cambium first resumes its activity, the more and more distant parts coming only successively into activity again.* It is precisely the parts nearest the fully expanded leaves and the maturing terminal buds in which the cambium also first ceases to be active. In plants which form no terminal buds —such as roses, briars, etc.—the cambium continues to be active so long as the temperature, moisture, and other external conditions make growth possible. The cambium cells divide more or less early, and a larger or smaller number of times. To a considerable extent at least this is according to the behavior of the parts developing from the opening buds. The living cells in rapidly growing leaves and elongating internodes, demanding much food and water, stimulate by this demand the earliest cells cut off by division of the cambium cells to grow to such size and to take on such characters that they will best conduct what is needed above. If the ground is so dry that only insufficient quantities of water can be absorbed, or if in the preceding year only insufficient quantities of food were made and stored, the parts coming from the opening buds will develop less rapidly or less perfectly in size, etc., and will be able to exert and will exert less of a stimulating demand upon the conducting tissues for food and water than in a better season. In this way nutrition affects everything, the formation of wood as well as the development of new organs. In the various living cells composing the embryonic organs in the bud, the impulse to grow is given by returning favorable conditions. Warmth, light, moisture, etc., stimulate the cells to grow, to divide, to grow again, to differentiate, etc. These cells, stimulated by purely physical influences from outside themselves, develop needs proportioned to their physiological activities. The needs must be met, if the cells are to continue their activities, by materials drawn from their neighbors. So this demand, extending from cell to cell by the osmotic transfer of nutrient solutions, presently reaches the living cells adjoining the conducting elements, the cambium and its daughter cells. According to the demand, the stimulus, thus exerted, these daughter cells develop into the so-called "spring wood."

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* Jost, L. Beobachtungen über den zeitlichen Verlauf des Dickenwachsthums der Bäume. Ber. d. Deutsch. Bot. Gesellsch., Bd. X., 1893.

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* Jost, L. Beziehungen zwischen der Blattentwickelung und der Gefässbildung in der Pflanze. Bot. Zeitung, 1893.

The hypothesis thus outlined would be worthless if it were not for the early growth of the roots which makes possible the supply of the relatively large volume of water demanded by the parts coming from the bud. Goff* has recently shown that growth of the root begins in the spring before there are any signs of growth in the parts above ground. Thus the plant is early provided with the absorbing agent needed. This growth of the root also must be regarded as the irritable response to the stimulus exerted upon it by the moisture and the increasing warmth of the soil.

The other half of the annual ring remains to be accounted for. What has already been said regarding the effect of increasing the mechanical strains to which growing parts are subjected (see pp. 174, 187–8) prepares us for an hypothesis, deserving more experimental tests, to account for the change in the character of the season's growth of wood. After the buds open, the leaves expand and grow, the internodes lengthen, and all the parts and their component cells attain their definitive dimensions, weights, etc. As a result, the mechanical strain upon the parts behind increases. It increases not only with the weight and with the change in position of the weight, which produces a greater leverage, but also with occasional sudden and often very great additions to the weight by wind and rain. Meantime there is little or no increased demand for food, and transpiration, being controllable by the stomata, is not likely to increase greatly. There is ordinarily, therefore, no great addition to the conducting system (see pp. 123–4).

Strengthening tissues—fibres, tracheids, thick-walled elements—are formed by the differentiation of the young cells derived from the cambium. From Hegler's investigations (p. 187) it is evident that strengthening tissues develop according to the strain to which a part is subjected, that an increasing strain is accompanied by the formation of more and stronger mechanical tissues, and that this development is a response to irritation. We have only to apply these conclusions to the changes taking place in growing wood as the season progresses to gain an idea as to one of the most important influences contributing to the formation of "autumn wood."

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* Goff, E. S. The resumption of root-growth in spring. Wisconsin Agric. Exp. Sta., 15th Annual Report 1898.

Ordinarily only one ring is added to the wood each year. Many woody plants, if defoliated by frost, caterpillars, etc., so early in the season that growth has not ceased, will open their latent buds, and develop a second set of leaves. Under these conditions, with the sudden increase in the demand for new conducting tissues, the young derivatives of cambium will develop into elements resembling but not quite equalling those of normal "spring-wood." In this way woody plants may form in nature two rings of wood in a single year. It is claimed* that "spring" and "autumn" wood may be found repeatedly alternating with one another in a single season's growth in pine, if only during the growing season there are repeatedly alternating and sharply contrasting rainy and dry periods. Pfeffer's caution† "that an apparently similar result may sometimes be produced in various ways" applies to this observation as well as to experiments.

The careful study of plants subject to the attack of gall-insects and other pests should throw light on the relation of the growth of wood to the demand made upon it. For example, cross-sections of the younger branches of Monterey Pine (*Pinus radiata*) which have been attacked by the leaf-galling insect *Diplosis pini-radiatæ*,‡ show abnormalities in the vascular tissues. Instead of the clearly marked annual rings of wood, these branches have semi-annual rings which correspond in size, position, and composition with the times at which the plant is attacked by the gall-insect, at which the morbid growth begins and ends, and with the differences in the activities of the galled leaves from those which are normal.

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* Lutz, K. G. Beiträge zur Physiologie der Holzgewächse. Fünfstück's Beiträge z. wiss. Bot., Bd. I., 1897.

† Pfeffer, W. Pflanzenphysiologie, 2te Aufl., Bd. II., p. 274, 1901.

‡ Papers by Cannon, W. A. The Gall of the Monterey Pine. American Naturalist, vol. 34, 1900; and Miss Mills in Entomological News, vol. XI., 1900.

The formation of wood and of its different kinds and elements in a season is affected by all the vital activities of the plant and all the external influences which bear upon it. The character of the wood is not the result of any one set of factors. At the same time that we must constantly recognize that the living plant is sensitive to a great many influences and that it responds to these, we may distinguish in the complex of influences some which are more effective than others. We may therefore accept, at least until a better one is advanced, this hypothesis: the two kinds of wood in the year's growth are formed in their different ways in response to the different demands, or stimuli, brought to bear upon the cambium and its young derivatives; the "spring wood," composed of large elements, essentially for the conduction of liquids; the "autumn wood," composed of small and thick-walled elements, essentially for mechanical strength; and between these two, the wood which is both "spring" and "autumn" in character, formed when there is still need of more conducting tissues and when the need of strengthening tissues is already beginning. So we have the adaptation of the wood to the different needs of the plant in different parts of the growing season, the adaptation being accomplished through the irritability of the growing and differentiating cells.

INFLUENCE OF GRAVITATION.

So far we have studied mainly the effects of evidently mechanical influences upon the living organism. It is, however, sensitive to many other influences, some of them quite as important. Of these only one is constantly and uniformly operative—the force of gravitation. The plant may change, by growth and movement, the relation of its parts to the force, but the amount of force acting upon the plant continues the same. The other influences are variable, periodic, or occasional. The mechanical influences so far discussed may be said to control growth by limiting it. The influences which we are about to study control growth by directing it. Yet this distinction is suggestive rather than exact, and must not be accepted without reserve.

The action of gravitation may be considered from its effects on the kind, rate, and direction of growth, and on the position, of plants. Gravity exerts upon all objects a pull toward the centre of the earth. This pull is proportioned in intensity to the weight (mass) of each object, the heavier the object the stronger the pull. The pull is resisted more or less completely by the medium in which the objects are. An object in a fluid is buoyed up with a force equal to the weight of the fluid which it displaces. Thus the downward pull of gravity upon a plant living submersed in fresh water is resisted by a force equal to the weight of the water which the plant displaces. This is 750–800 times greater than the force which an equal volume of air would exert. The average specific gravity of sea-water is 1.2. Hence a plant living in sea-water is supported still more, by a force 1.2 times greater than that of an equal volume of fresh water, and therefore 900–950 times greater than air. The parts of a plant growing in a solid medium, the soil, are completely supported. The soil will ordinarily support much more than the weight of the plants growing in it. It is evident, therefore, other things being equal, that the mechanical strength which the plant or plant-part must develop is proportioned to the fraction of the force of gravitation which is not balanced by the buoyancy or supporting power of the medium in which it lives. The force of gravity exerts by this means a direct influence upon the kind of tissue which the plant forms, the kind of growth which it makes. The force of gravity is one of the most important factors in the complex which constitutes the environment.

The rate of growth in most plants seems to be tolerably independent of gravity, other forces being more effective. Parts which normally stand in one direction may grow at a somewhat different rate when their position is changed. Also, when gravity is opposed by an equal or greater force, as can be done by a centrifugal machine, the rate of growth may be changed. But when the position of a plant is constantly changed or is changed at frequent and regular intervals, as by a regular or by an intermittent clinostat, the rate of growth does not seem to be materially affected.*

Gravity is one of the most important influences determining the direction of growth. It affects direction and kind much, the rate of growth little. Its action in directing growth is called *geotropism.* Those organs which grow toward the source of gravitation, downward, are said to be positively geotropic. Roots and rhizoids are positively geotropic organs. Stems which grow in the opposite direction, upward, are called negatively geotropic. Other organs, such as branches, which grow horizontally, are said to be diageotropic, while obliquely growing organs like lateral roots are called plageotropic. For reasons of convenience, roots have long been the favorite objects for the study of the effects of gravitation. Such horizontal organs as leaves owe their position quite as much to the influence of light as to gravitation. Though we may say that gravitation is the chief force directing the growth of stems and roots, it must be remembered that it is only the chief of several or many. The position which any part or organ finally assumes represents the combined influence of all of those forces to which it is sensitive and which act upon it.

It may be stated as a general rule that the stems and roots of higher plants, and the corresponding parts of many lower plants, tend to grow in opposite directions. Each organism begins as a single cell. Upon this one cell all the influences which affect the new plant are converged. The directions of growth and of division of this one cell are the result of these influences. In consequence of the first as well as of subsequent divisions, the different cells of the embryo are differently placed, some opposite to others. From this oppositeness in position there follows an oppositeness in behavior, which expresses a difference in the cells and organs themselves. It is easy and natural to suspect that the direction of the divisions of the fertilized egg-cell and of the first cells in the embryo bears a definite relation to the force of gravitation, and this appears in many plants to be really the case, but other influences may cooperate or predominate in producing the same effect, as, for example, in the ferns.* Whatever may be the origin in the embryo of the different responses which the different parts make, it is evident that, from the germination of the seed onward, the plant is sensitive to gravitation and is directed in its growth by it as well as by other forces.

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* For a discussion of this topic see Pfeffer's Pflanzenphysiologie, 2te Aufl., Bd. II., § 29, 1901.

The responses to the force of gravity are much better known than are the immediate effects of the force in the sensitive parts. Most of our knowledge and interest in the subject are due to Ciesielski,† Darwin,‡ Sachs,§ and Pfeffer §§ and their followers.

The young root is more highly differentiated, anatomically and physiologically, than its simple external appearance suggests. At the extreme tip is the cap, a protective covering of the "growing point." The "growing point" is a mass of permanent meristem which gives rise to all the root structures. Behind this is the region of evident growth, where the young cells are increasing in volume by the absorption of water from their older neighbors (see fig. 9, p. 168). Still further back and adjoining this region is the zone where, through the root-hairs, water is principally absorbed from the soil. If a young seedling with a straight root be laid so that its root will be horizontal, care being taken that the root remain moist, the tip will begin to turn downward within an hour from the time when its position was changed.* The tip is carried downward by the elongation and curvature that take place in the part most rapidly growing, 3–4 millimetres back of the tip. In this case gravity acts as a stimulus. Gravity cannot be the sole force pulling the tip into the soil, for the tip is too light, and the resistance of the soil is too great, for any such result.

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* See Goebel, K. Organographie der Pflanzen, pp. 188+, 1898. Campbell, D. H. Mosses and Ferns, 1895. McMillan, C. The orientation of the plant-egg and its ecological significance. Botanical Gazette, vol. 25, 1898.

† Ciesielski, T. Untersuchungen über die Abwärtskrümmung der Wurzel. Beiträge z. Biologie d. Pflanzen, Bd. I., 1872.

‡ Darwin, C. The Power of Movement in Plants, 1880.

§ Sachs, J. von. Different papers from 1873 to 1879, collected in his Gesammelte Abhandlungen über Pflanzenphysiologie, Bd. II., 1893, and in his Lectures on the Physiology of Plants. Eng. transl., 1887.

§§ Pfeffer, W. Geotropic sensitiveness of the root-tip. Annals of Botany, vol. VIII., 1894.

Darwin believed that the tip of the root, like the brain, is a sense organ, receiving the stimulus of gravitation and sending back to the elongating part the impulse to respond to it. Sachs and others contended that only the growing part received the stimulus and acted upon it. For years the matter stood thus, and Rothert,† very carefully reviewing the whole subject, had just published his opinion that it could not be decided experimentally when Pfeffer‡ announced the results of the ingenious experiments conducted under his direction by Czapek.§ In order to decide the matter it was necessary to employ means which would not in any way injure the root or introduce any new factors into the experiment; decapitation, wounding, and the other devices resorted to before being obviously open to objections serious enough to invalidate the conclusions drawn from experiments involving such procedure. This was accomplished by taking advantage of the plasticity of the growing tip, causing the roots to grow into tubes, 3–4 millimetres long, of thin glass, bent in the middle at a right angle. While the tips were growing into these tubes, the plants were revolved on a clinostat, so that no directive geotropic irritation should be set up. "If now a specimen," prepared as shown in the accompanying figure, "is placed so that the terminal part points vertically downwards, whilst the rest of the root is horizontal, no geotropic curvature takes place. This, however, always took place, and with about the same promptness as in straight roots, when the terminal portion was placed horizontally, or in general at an acute angle with the normal position. From these experiments it follows that the root thus treated is perfectly capable of reaction. . . . By this means therefore it is proved with the most perfect certainty, that in an uninjured root only the root-tip is geotropically sensitive." With this is also proved that from the part which is sensitive —the part of the root with the largest amount of living protoplasm in proportion to its volume — the stimulus is transmitted to cells capable of responding to the stimulus. These are the cells at that time increasing in volume, growing. The position of the tip is determined by its own sensitiveness, but its position can be changed, except by artificial means, only by the action of the responding part. The stimulus is transmitted from living cell to living cell. The transmission takes time, but the interval, known as the latent period, between exposure and response to the stimulus, is necessarily employed in preparing to execute the response as well as in transmitting the stimulus. The latent period may mean still more, but at least it means these two things.

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* For experiments on roots, seeds may best be germinated in damp tannin-free sawdust. (Stone, Bot. Gazette, XIX., 1894.) Many experiments are described in the laboratory manuals previously named.

† Rothert, W. Die Streitfrage über die Function der Wurzelspitze. Flora, 1894.

‡ Pfeffer, W. Über die geotropische Sensibilität der Wurzelspitze. Sitzungsber. d. K. Sächs. Gesellsch. d. Wissensch., Sitzung vom 2ten Juli, 1894. Geotropic sensitiveness of the root-tip. Annals of Botany, vol. VIII., 1894.

§ Czapek, F. Untersuchungen über Geotropismus. Jahrb. f. wiss. Bot., Bd. XXVII., 1895.

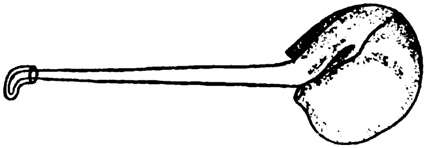

Figure 14. Root-tip in bent glass tube. (From Czapek.)

The transmission of the stimulus cannot be understood until it is known in what the stimulus exerted by gravity consists and what it does in the sensitive cells. All the ponderable parts of an organism and of a cell are subject to the physical pull of gravity. From this it follows that while these parts are in place their position is maintained as the result of the activity of living protoplasm. When the position of these parts is changed, either by the living protoplasm or by means outside of it, the relations of the parts and of the protoplasm to gravity are also changed. The force of gravity acts constantly. Therefore, whether the ponderable parts of a cell are changed or are constant in position, they and the protoplasm are constantly influenced by gravity. Only when there is a change in the relation of the parts to gravity is the protoplasm called upon to change its response. The action of gravity in a cell and upon its parts must be the same as upon any ponderable substance. The heavier (or lighter) the substance, the greater (or less) its specific weight as compared with the protoplasm in which it is imbedded, the more promptly will it exert a different pressure upon the protoplasm and change in position when the position of the cell is altered. In every living cell there are solid particles of greater or less size, living or lifeless, presumably differing among themselves and from the protoplasm in weight. In certain plants, *e.g.* some Desmids, in rhizoids of Chara,[*] in the starch-sheath of stems and in the root-cap, etc., of higher plants,[†] solid particles are conspicuous in size or arrangement. The force of gravity will, however, act similarly, though less evidently, upon the solid contents of all cells.

The reaction of the living protoplasm to the pull of gravity is very different from that of lifeless material. The reaction may show itself in a variety of ways, chemical and physical. Czapek[‡] has shown that a chemical change takes place in root cells stimulated geotropically. In the periblem cells of sensitive root-tips there is present, in larger quantity than elsewhere, a readily oxidized substance, perhaps also another which is a vehicle of oxygen. In the irritated root-tip, and directly in proportion to the irritation, the amount of aromatic oxidizable substance increases and the substance or substances serving as a vehicle for oxygen decrease. This transfer of oxygen from one compound to another within the cell is accomplished not by gravity but by the living protoplasm stimulated by gravity.

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[*] **Giesenhagen, K. Über innere Vorgänge bei der geotropischen Krümmung der Wurzeln von Chara. Ber. d. Deutsch. Bot. Gesellsch., XIX., 1901.**

[†] **Haberlandt, G. Über die Perception des geotropischen Reizes. Ber. d. Deutsch. Bot. Gesellsch., Bd. XVIII., 1900. Über die Statolithenfunction der Stärkekörner. *Ibid.*, Bd. XX., 1902. Němec, B. Über die Art der Wahrnehmung des Schwerkraftreizes bei den Pflanzen. *Ibid.*, Bd. XVIII., 1900. Über die Wahrnehmung des Schwerkraftreizes bei den Pflanzen. Jahrb. f. wiss. Bot., Bd. XXXVI., 1901. Noll, F. Über Geotropismus. *Ibid.*, Bd. XXXIV., 1900. Zur Controverse über den Geotropismus. Ber. d. Deutsch. Bot. Gesellsch., Bd. XX., 1902.**

[‡] **Czapek, F. Ein mikroskopischer Befund an geotropisch gereizten Wurzeln. Ber. d. Deutsch. Bot. Gesellsch., XV., 1898. *Also* Jahrb. f. wiss. Bot. Bd. 32, 1898.**

The transmission of a stimulus which caused only mechanical changes in the stimulated cell would be very difficult to conceive. On the contrary, when there is a change in the amount or the composition of diffusible substances, it is much easier to form some notion of the means by which the impulse to grow in a definite way is given by the meristematic cells at the root-tip to those in the growing region behind. Any change of this sort in one cell is necessarily followed by corresponding diffusion currents between this cell and its neighbors more and more remote. Wherever a new substance enters the living protoplasm of a cell it will affect the protoplasm chemically or physically, thus producing a stimulus. The irritated periblem cells of the root-tip give up by diffusion the changed substances which they have formed. Finally those cells in the growing zone are reached by the diffusing compounds, and they change the direction if not also the rate of growth of the organ.

Diffusion undoubtedly occurs between the sensitive cells of the root-tip and the cells more or less remote. The transmission of an impulse by diffusion alone is not rapid, and it is difficult to prove. To avoid both of these objections Němec* has recourse to protoplasmic fibrils to which he attributes the function of conducting stimuli from cell to cell. These fibrils can be seen in suitably prepared fixed material and in certain living cells (*e.g.* stamen and slime hairs of *Tradescantia*), both in tissues which are irritable and which exhibit visible reactions to stimuli, and also in tissues in which no response to stimuli has ever been detected.* Since we conceive all living cells to be affected by external influences, whether they give a response which can be seen at any time or not, there is every reason to believe that all the living cells in a body are connected together. Indeed, Strasburger's investigations go far toward proving that such is really the case.† By Němec's fibrils and Strasburger's continuity of protoplasm the living parts of a plant are united in one system. Granting this to be the case, it is nevertheless difficult to see how these structures convey a purely mechanical stimulus like that of gravitation. Němec's fibrils suggest the nerve structures in animals. Like these structures, their manner of working is a mystery. We may therefore cling to our diffusion hypothesis as comprehensible, if difficult of proof, leaving the future to determine the value and the functions of protoplasmic fibrils and protoplasmic continuity.

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* Němec, B. Die Reizleitung und die reizleitenden Structuren bei den Pflanzen. Jena, 1901.

Sachs asserted that when a root-tip is horizontal it is in position to be most strongly stimulated by gravity, and that then the curvature of the growing region will be most rapid and most pronounced. Until Czapek ‡ determined the necessary duration of the stimulus, Sachs's assertion was unchallenged. Czapek ascertained that the root-tips of various plants require from fifteen to fifty minutes' exposure to the action of gravity in order to bend. The longer the exposure, the more pronounced in rapidity and angle is the bending. Thus roots of *Lupinus albus* will bend if laid horizontal for twenty minutes, but the maximum effect will follow an exposure of four hours. When the root-tip points upward at an angle of 45°, not when it is horizontal, the root bends most, the time of exposure and other conditions being the same. Above this angle, the spontaneous growth-movements, known as nutation or circumnutation, interfere with the action of gravity. Czapek's conclusion is supported by a study of grass-haulms.*

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* Haberlandt, G. Über Reizleitung im Pflanzenreich. Biolog. Centralblatt, XXI., 1901. Über fibrilläre Plasmastructuren. Ber. d. Deutsch. Bot. Gesellsch., XIX., 1902.

† Strasburger, E. Über Plasmaverbindungen pflanzlicher Zellen. Jahrb. f. wiss. Bot., Bd. 36, 1901.

‡ Czapek, F. Untersuchungen über Geotropismus. Jahrb. f. wiss. Bot., Bd. 27, 1895. Weitere Beiträge zur Kenntniss der geotropischen Reizbewegungen. Jahrb. f. wiss. Bot., Bd. 32 1898.

When the root-tip is stimulated by the action of gravity a bending takes place further back, in the region which is most rapidly elongating. This region, called the motor zone, can bend only if there are differences in the rate of growth or in the tissue tensions in its different parts. It is not necessarily the case that all roots behave alike in the means any more than in the manner of curvature, although it seems probable that in roots of similar structure the mechanics of curvature will be similar. This may account in part for the diverse views regarding the mechanics of geotropic curvature. Thus, according to Ciesielski,† the cells of the lower (concave) side of the root are forcibly compressed, even wrinkled, by the more than average growth of the cells of the upper (convex) side. Sachs ‡ denies that the cells of the upper side always grow faster, and attributes the pronounced bending to the diminished growth rate of the cells of the lower side. MacDougal,§ employing the imbedding methods now in general use but unknown to Sachs when he wrote on this subject, comes to essentially the same conclusions as the great master in plant physiology more than twenty-five years before. Pollock,¶ studying curvatures induced by injury (traumatropic) instead of by gravity (geotropic), concludes that the mechanism of root-curvature consists in changed tissue-tensions in the stimulated roots, the normal tension between cortical parenchyma and axial cylinder increasing on the upper (convex) side and decreasing on the lower (concave) side. Though this last view may be correct as regards some if not all roots, it must be conceded that growth makes permanent the changes induced by irritation, whether these changes in direction are first effected by changes in the tissue-tensions of the motor zone or by growth itself.

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* **Pertz,** Miss D. F. M. On the gravitation stimulus in relation to position. Annals of Bot., XIII., p. 620, 1899.

† **Ciesielski,** Th. Untersuchungen über die Abwärtskrümmung der Wurzel. Cohn's Beitr. z. Biol. d. Pflanzen, Bd. I., 1871.

‡ **Sachs,** J. von. Gesammelte Abhandlungen, Bd. II., p. 852.

§ **MacDougal,** D. T. The Curvature of Roots. Bot. Gazette, vol. 23, 1897.

¶ **Pollock,** J. B. Mechanism of root-curvature. Bot. Gazette, vol. 29, 1900.

What has been said about the irritability and means of response of roots which grow vertically (orthotropic), applies equally to lateral roots which grow obliquely (plagiotropic). The difference between these organs lies in their different relations to irritation by gravity. They may not differ in sensitiveness, but they will respond in different degrees to the same force. We may conceive this to be due to the different balances of all the influences to which the two kinds of roots are subject. If both lateral and primary roots grew vertically, they would interfere with one another in position and in functions, failing to attain their utmost usefulness and irritating one another by their products. This may be the main factor in determining the position of lateral in relation to primary roots. The response of lateral roots to the stimulus of gravity will be changed when the primary root is removed or so injured that its further vertical growth is impossible. The lateral roots will then bend down and one or more will attempt to take the place in position, direction of growth, etc., of the primary root. The relation of any organ to any one influence or combination of influences depends upon the relation of all the other organs to each one of the influences composing the total to which the organism is subject.*

Among stems as among roots there are erect (orthotropic) and horizontal (plagiotropic) organs, differing from one another, not in their sensitiveness or in the efficiency of their response to gravity, but in their relation to the force. In the ordinary orthotropic stem, unlike the root, there is no separation into sensory and motor zones, though Francis Darwin† has shown, in the seedlings of certain grasses, that the first leaf-sheath is sensitive to gravitation and the bending is accomplished only by the segment of stem immediately below. In ordinary orthotropic stems geotropic sensitiveness and response are possible only in elongating parts, and since the nodes and internodes soon cease to grow in length, geotropic phenomena soon cease. In such stems the cortical parenchyma, uniform in structure and usually containing chlorophyll, is the sensitive tissue, all the other tissues cöoperating in the response to the stimulus. In grass haulms, on the other hand, there being a persistent meristem at the base of each internode and in this no visible differences among the cells, we may assume that the whole meristem is sensitive as well as responsive. When a grass haulm is laid prostrate by wind or rain, the meristem cells on the lower side of each internode begin again to divide, growth is resumed, and by this means the parts nearer the tip are gradually carried again into the vertical position.

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* Consult Czapek, *loc. cit.*, and Schober, Das Verhalten der Nebenwurzeln in der verticalen Lage. Bot. Zeitung, 1898.

† Darwin, F. On geotropism and the localization of the sensitive region. Annals of Bot., XIII., 1899.

Prostrate and underground stems and branches, and especially leaves, though sensitive to gravity and assuming very definite positions when acted upon by gravity alone, are so much more strongly affected by light that their position, as well as their form, size, and structure, must be ascribed mainly to its influence rather than to gravity (see pp. 214–215).

After the growing (motor) zone has executed the response to the stimulus received by the organ, the whole organ returns, like the sense organs and muscles of an animal, to that state of delicate balance and readiness in which the first stimulus found it. If such a return is made impossible by continued stimulation, the response will be continuous until fatigue, insensibility, and impotence are produced, or until the response carries the organ into such a position that other influences will modify or prevent any further response. This has been shown by Frank,* Darwin,† and Copeland,‡ who found that, on confining the sensitive part to a horizontal position, an almost continuous bending takes place. Similar to this is Elfving's observation* that when a fully grown grass internode is revolved horizontally on a clinostat, its meristem resumes its activity, its cells divide uniformly under the stimulus of gravity applied successively to all its parts, and the internode passes through another period of growth in length.

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* Frank, A. B. Beiträge zur Pflanzenphysiologie: I. Über die durch die Schwerkraft verursachten Bewegungen von Pflanzentheilen. Leipzig, 1868.

† Darwin, F. On geotropism and the localization of the sensitive region. Annals of Bot., XIII., 1899.

‡ Copeland, E. B. Studies on the geotropism of stems. Bot. Gazette, XXIX., 1900.

The force which a geotropically bending organ exerts is manifestly considerable, *e.g.* that employed in restoring a prostrate grass haulm to the vertical position. The force thus exerted is developed by the growing and bending part, and we have seen (p. 176) that growing organs may exert force equalling a pressure of ten atmospheres. As in ordinary growth, stems and roots bending because of geotropic stimulation will develop only the amount of force needed to accomplish the bending. This has been proved experimentally by Meischke.† He ascertained the force ordinarily exerted by geotropically bending parts, and found that, when compelled to do so, they developed from several to many times this force in order to accomplish the bending. Thus—

Grass internodes can develop	4	times the ordinary bending force.
Cucurbita seedlings	18	"
Lupinus "	17	"
Phaseolus "	28	'
Helianthus "	30	'

If any evidence of geotropic stimulus were needed, more striking than the geotropic curve itself, these figures, indicating the increase in power under stimulus, would furnish it.

INFLUENCE OF LIGHT

Light as a form of energy does certain kinds of work and accomplishes certain chemical changes within as well as outside living cells. Living protoplasm is composed of chemically unstable substances. Some of its constituents and organs bear also definite physical relations to light. Light is neither constant nor uniform in amount, its direction and intensity change, hence its action upon the same organ or organism is different, may even be opposite, at different times. Light affects the living protoplasm through the chemical processes and physical conditions of the cell at all influenced by light. Sunlight and the ordinary artificial lights are composed of rays of different sorts which separately affect the substances, living and lifeless, exposed to them. The effect of ordinary white light is then the sum of the effects of its constituent rays. These rays, visible and invisible, fall into three classes, the thermal or heat, the luminous or light, and the actinic or chemical rays. Their effects are partly suggested by their names. The luminous rays, being the ones most concerned in food-manufacture, affect the protoplasm in ways which we have already studied (see pp. 53–57). The heat rays we have also examined in their relation to transpiration, etc. (pp. 136–151), and we shall study them further in the succeeding section of this chapter (pp. 219–222). We have here to consider mainly the influence of the visible and invisible ("ultra-violet") chemical rays.

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* Elfving, F. Verhalten der Grasknoten am Klinostat. Öfversigt af finska Vet. Soc., Förhandlinger, Bd. 26, 1884.

† Meischke, P. Über die Arbeitsleistung der Pflanzen bei der geotropischen Krümmung. Jahrb. f. wiss. Bot., Bd. 33, 1899.

Some idea as to why and how actinic rays affect living protoplasm so strongly—in other words, why living protoplasm is so very sensitive to light—may be gained by considering how powerfully those rays influence lifeless substances and many processes taking place under the more readily understood conditions prevailing outside the living organism. For example,* olive oil oxidizes when exposed to light, oxalic acid in solution will break up into carbon-dioxide and formic acid in the light, alcoholic solutions of chlorophyll decompose more rapidly in light than in darkness, and many enzyms are destroyed by exposure to light. These are all organic compounds occurring in plant cells. The most significant in the list are the enzyms. Enzyms accomplish the conversion of insoluble substances in the cell into soluble, portable, and useable compounds (see pp. 29-30). If the work of the enzyms is interfered with by light, the functions of the cell must be altered or become deranged. The substances composing the living protoplasm may also be as sensitive to light as its products. The sensitiveness to light of the compounds in and perhaps composing their cells is the reason for the sensitiveness of living organisms to light.

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* Davenport, C. B. Experimental Morphology, Part I., pp. 162–5, 1897.

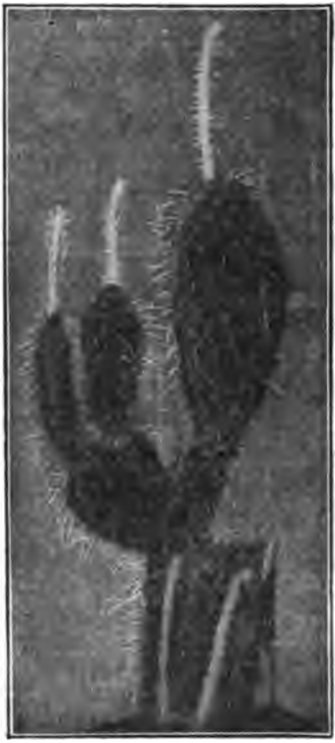

Figure 15. Branch of Cactus, the young parts of which grew in darkness. (From Goebel.)

The influence of light, like the influence of gravity, may show itself in the kind, rate, and direction of growth, and in the position of the organ and organism.

Plants kept in darkness will be longer than plants under normal illumination. Seeds sprouted in darkness, and seedlings growing where no light falls upon them, grow under the influences of all other forces than light. When the influence of light is wholly eliminated, root, stems, and branches grow longer but are proportionally more slender than in ordinary sunlight, the leaves are smaller and weaker, flowers do not form (see pp. 271-4). That stems are more slender and mechanically weaker in darkness than in light may be due to the less than normal weight of the small weak leaves—to the absence of mechanical strain (see p. 188). The leaves require a certain amount of light in order properly to develop the food-manufacturing tissues. Yet, comparing the total growth of plants of the same species in light and in darkness, it will be clear that the growth is greater in darkness so long as the plant is adequately nourished. Light retards the growth of those organs which do not depend upon it for energy for food-manufacture.

The form as well as the size of parts is greatly influenced by light. If a branch of cactus, *Opuntia*, be potted and kept in darkness, the buds will develop into branches which are small and cylindrical, while the branches formed in the light are larger and flat.[*] *Marchantia gemmæ*, germinated in the light but on a clinostat, develop in two months into small erect tubular plants, wholly unlike the flat expanded thalli which form when light and gravity act normally.[†]

The daily periodicity of light and darkness are almost coincident with the daily periodicity in growth-rate. This was first shown by Sachs,[‡] who devised machines (auxanometers) for autographically recording the growth of plants during extended periods. These records show that the rate of growth in length, of plants furnished with all the food they need, will reach its maximum about sunrise, its minimum about sunset. That growth is not most rapid when there is least light, or slowest when the light is strongest, shows that the effect of light, like that of gravity, is cumulative (p. 204). Maximum growth-rate and minimum temperature almost coincided in Sachs's experiments, but this indicates, not that coolness favors growth, but that Sachs did not make his experiments at constant temperatures. Sachs's experiments, repeated at constant temperatures, show that the maximum and minimum growth-rates occur at approximately the same times as before, and that light and not heat is the predominant influence in controlling the rate of growth.

It is claimed that light favors the growth of the vegetative organs of submersed aquatics. A certain minimum amount of light is required by them to carry on the essential process of food-manufacture. A larger amount acts as a stimulus to the formation of reproductive organs (pp. 264-8). Otherwise the relations of these plants to light are similar to those of land plants. Since the water and the materials at the bottom of a natural body of water absorb light, plants living in such a situation receive less light than the plants living on the bank near by. Plants living on or over a dark or black bottom receive light only or mainly from almost vertically above. The quality as well as the quantity of light reaching water plants differs from that falling upon plants in the air. Water absorbs the different kinds of rays unequally, the luminous rays least, the actinic rays more. Whipple* cultivated diatoms in bottles at dif-

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[*] Vöchting, H. Über die Bedeutung des Lichtes für die Gestaltung blattförmiger Kakteen. Jahrb. f. wiss. Bot., Bd. 26, 1894. Goebel, K. Organographie, I., pp. 211+, 1898. *Also* Flora, Bd. 80, 1895.

[†] Czapek, F. *l. c.*, 1898, p. 261, 271, etc.

[‡] Sachs, J. von. Über den Einfluss der Lufttemperatur und des Tageslichtes auf die stündlichen und täglichen Änderungen des Längenwachsthums (Streckung) der Internodien. Arb. d. Bot. Inst., Würzburg, 1872. Gesammelte Abhandlungen, Bd. II., 1893.

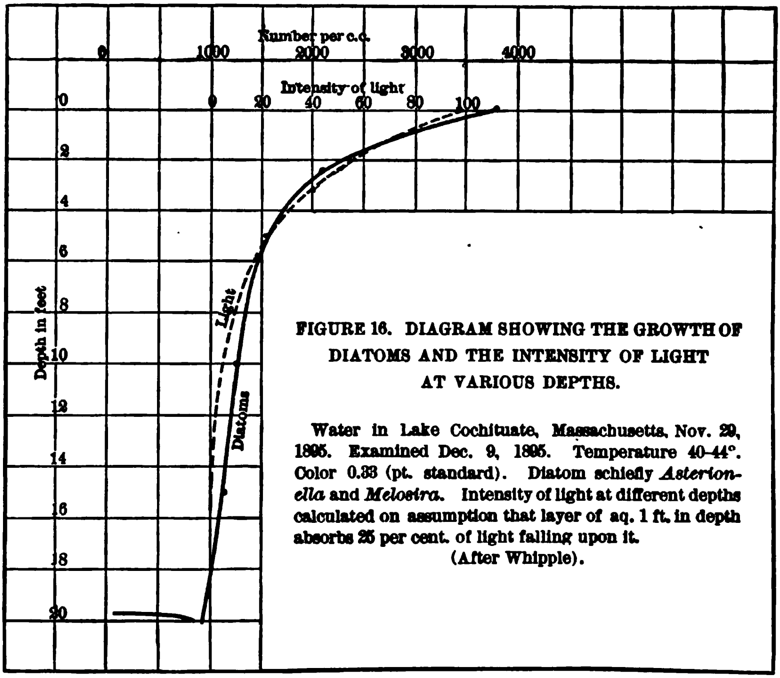

FIGURE 16. DIAGRAM SHOWING THE GROWTH OF DIATOMS AND THE INTENSITY OF LIGHT AT VARIOUS DEPTHS.

Water in Lake Cochituate, Massachusetts, Nov. 29, 1895. Examined Dec. 9, 1895. Temperature 40-44°. Color 0.33 (pt. standard). Diatom chiefly *Asterionella* and *Melosira*. Intensity of light at different depths calculated on assumption that layer of aq. 1 ft. in depth absorbs 25 per cent. of light falling upon it. (After Whipple).

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* Whipple, G. C. Some experiments upon the growth of diatoms. Technology Quarterly, vol. IX., 1896. *Also* Microscopy of Drinking Water, 1901.

ferent depths in a reservoir. Taking the numbers present as an index of the suitableness of the illumination at different depths—a standard not above criticism—the largest number, and inferably the best illumination, are found a few inches below the surface. The accompanying diagram indicates the results of the experiment. On the surface, where there was no absorption of light, and where the organisms could therefore receive most light, the growth (*i.e.* the reproduction) was less than when a thin layer of water absorbed the actinic rays.

Certain seeds and spores appear to germinate better, and perhaps only, in light.* The European mistletoe (*Viscum album*), the seeds of some grasses, and the spores of some of the vascular cryptogams are said not to germinate in darkness. In these cases we have the stimulating influence of light upon processes which precede growth (*e.g.* respiration†). After their germination, the influence of light upon growth is the same as in other plants.

The influence of light upon the rate of growth is evident from the foregoing; light lowers the growth-rate. If unequal amounts of light fall on different parts of a growing organ, the growth of the organ will be unequal. By this means the direction of growth of an organ or organism is influenced by light. The stems of plants growing indoors near a window turn toward the light, the leaves spread themselves at right angles to the incident rays, the roots (when visible at all) turn away from the light. The behavior of the parts of such plants is readily accounted for on the basis of what has already been said. The growing cells on the side of the stem away from the window receive less light and are less checked in growth than those on the opposite side, and hence push the tip of the stem over toward the window. The influence of light upon the direction of growth, though we see that it is due to the effect of light on the rate of growth, is known as *heliotropism* or *phototropism.*

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* Davenport, C. B. Experimental Morphology, Part II., pp. 423 - 5, 1899.

† Kolkwitz. R. Über den Einfluss des Lichtes auf die Athmung der niederen Pilzen. Jahrb. f. wiss. Bot., Bd. 33, 1898.

Most stems are positively heliotropic, that is, bend toward light of ordinary intensity and composition. The English Ivy (*Hedera*), to a certain extent *Ampelopsis*, the touch-me-not (*Impatiens*), the garden nasturtium in its older stages (*Tropæolum majus*),* and some other plants, are negatively heliotropic toward intense light, though not to light of lower intensity. These are plants which either climb against objects which absorb much light and hence appear dark, or thrive best in comparative shade. The behavior of the roots which attach these climbers to their supports is consistent with the relation of most roots to light.

Roots are not markedly sensitive to light, light serving, as a rule, only to supplement gravity. So much more does gravity influence the direction of growth of roots that the influence of light is scarcely apparent† until all parts are uniformly subjected to gravitation by means of the clinostat.

Underground and other horizontally growing stems exhibit a peculiar adjustment to the influences of gravity and light, their position being the resultant of their reactions to these two opposite stimuli. The prostrate shoots of *Rubus*,‡ the runners of strawberry, etc., and the root-stocks of *Nuphar*§ are examples. Goebel shows that the root-stock of *Nuphar luteum* creeps horizontally in the mud, possessing at this time a somewhat dorsi-ventral structure. If covered with soil, such a rhizom would bend, grow vertically upward until it came to the light, the structure of the vertical part being radial. At the surface of the soil it would bend to the horizontal and grow through the muddy twilight as before.

The position and direction of growth of leaves is also a resultant of the two forces, gravity and light. If a plant is revolved horizontally around its long axis on a clinostat, thus exposing it uniformly on all sides to gravity and to light, its leaves will assume no uniform and definite position. However, when the plant is illuminated from one direction only while it is being revolved on the clinostat, the leaves will take a very definite position, such that the blades are at right angles to the incident rays.

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* Wiesner, J. Die heliotropischen Erscheinungen. Denkschrift der Wiener Akademie, Bd. 39 u. 43, 1878 u. 1880.

† Wiesner, J. *l. c.*

‡ Czapek, Fr. *l. c.* 1898, p. 245, 257, etc.

§ Goebel, K. Organographie der Pflanzen, I., p. 198, 1898. Stahl, E. Einfluss des Lichtes auf den Geotropismus einiger Pflanzenorgane. Ber. d. Deutsch. Bot. Gesellsch., Bd. II., 1884.

Light and gravity work very closely together in determining the direction, size, and even form into which organs and organisms grow. When one influence is reduced or excluded, *e.g.* light, there is a change in the organism in its relations not only to the influence excluded but also to those that remain. The influence of the one force or the other may predominate in one set of organs—as the roots are affected mainly by gravity, the leaves mainly by light—or they may be nearly or quite balanced. Profoundly as they affect the parts sensitive to them, these forces are only factors in the complex of influences, mechanical, nutrient, and other, which together determine the character of the organism. No figures as to the relative effectiveness of gravity and light acting upon the whole organism can be given, yet Czapek* presents some figures of the same objects under like conditions, indicating the minimum times of exposure for reactions to gravity and light.

	GEOTROP.	HELIOTROP.
Avena sativa, (etiolated)	15 minutes	7 minutes
Sinapis alba, hypocotyl (etiolated)	15 "	10 "
Beta vulgaris, " "	15 "	10 "
Zea Mais, primary root	20 "	—
Helianthus annuus, hypocotyl	20 "	20 "
Phaseolus multiflorus, epicotyl	50 "	50 "
Phycomyces nitens, sporangiophore	15 "	7 "

The direction of locomotion in motile plants is influenced more by light than by any other one influence except that of food or of other stimulating compounds. An organism able to move about will finally reach the position in which it is most favorably affected by all the influences to which it is susceptible. Other positions might be more favorable for separate influences, but, the influences continuing constant, the position occupied may be regarded as the best. If the influences remained constant we could conceive that the sensitive motile organism, which had come into the place and position in which the balance of stimuli was most favorable, would never move again. The influences are all changing, except gravity, and hence the organism is exposed to changing degrees and kinds of stimulation. We may imagine that the movements of freely motile organisms indicate three things—the rate at which the stimuli change, the degree of sensitiveness, and the rate of response of the organism. The stimuli may change very rapidly, but a dull or feeble organism will not move correspondingly fast. Conversely, an extremely sensitive and strong organism will be in rapid motion even when conditions are in the main unchanged. But since conditions are not absolutely identical at two different points, locomotion itself introduces the organism to new stimuli.

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* Czapek, F. Weitere Beiträge zur Kenntniss der geotropischen Reizbewegungen. Jahrb. f. wiss. Bot., Bd. 32, p. 185, 1898.

Diatoms, desmids, *Oscillatoria*, swarm-spores, ordinary bacteria, sulphur bacteria (both the red and the colorless), plasmodia, and many other motile organisms, move toward light until they reach the point of optimum illumination. Locomotion directed by light is called *phototaxis* or *heliotaxis*. Movement toward the light is said to be positive phototaxis, away from the light negative phototaxis. Most organisms are both positively and negatively phototactic, depending upon the degree of illumination to which they are exposed. Thus the various species of red sulphur bacteria now growing in my laboratory collect on the brightest parts of the jars in which they are living when the jars are on a table six feet from the nearest window, and on the less or least brightly lighted parts when the jars are on the window-sills.

Where locomotion, or at least a change in position of the whole organ or organism, is impossible, the organs of the cell are, in many cases, able to move in accordance with the intensity and direction of the light. This is shown most clearly by the movements of chromatophores.* The accompanying figures *a, b, c,* were drawn on a warm sunny morning from leaves of a moss (*Funaria*) growing under a bell-glass in the laboratory. Figure *a* is from a leaf taken from a plant when the dish was on a table six feet from the nearest window: the chlorophyll grains are against the upper and lower walls of the cells, presenting their maximum area to intercept the light. This is the typical daylight position. Figure *b* is from a leaf taken from a plant after the dish had been standing 5 to 10 minutes in brilliant sunshine on the window-sill inside the laboratory: the chlorophyll grains are against the lateral walls of the cells, presenting their minimum area to intercept the light. Figure *c* is from a leaf which had been kept in the dark for 5 to 10 minutes; the chlorophyll grains are against the lateral and *bottom* walls of the cells. These figures are drawn at the same magnification, but the cells and chromatophores differ considerably in size. Changes in position of the chlorophyll grains take place very rapidly, and the drawings must be

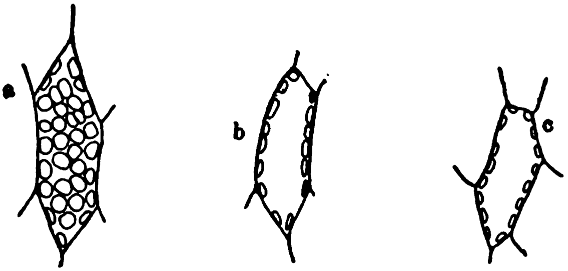

Figure 17. Cells from leaves of *Funaria Sp.*
a—cell from leaf in ordinary diffuse daylight.
b—position of chlorophyll-grains in intense light.
c—position of chlorophyll-grains in darkness.

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* Frank, A. B. Über die Veränderung der Lage der Chlorophyllkörner und des Protoplasmas in der Zelle und deren innere und äussere Ursachen. Jahrb. f. wiss. Bot., VIII., 1872. Stahl, E. Über den Einfluss von Richtung und Stärke der Beleuchtung auf einige Bewegungserscheinungen im Pflanzenreiche. Bot. Zeitung, 1880. Oltmanns, F. Über photometrische Bewegungen der Pflanzen. Flora, Bd. 75, 1892.

made rapidly and at once, else changes of considerable extent occur. Within two minutes after the darkened leaf is put on the microscope, the chlorophyll grains have gone halfway to the day position (*a*).

The behavior of the plate-like chromatophores of the alga *Mesocarpus* is similar.* When intense light falls upon a *Mesocarpus* cell, the chromatophore presents only its edge to the incident rays, but when the light is less intense the chromatophore bends, as in *c*, so that the greater part of it presents its profile to the light. Still less intense yet strong light induces the position indicated in *b*, and light of only moderate intensity or less is indicated by the chromatophore being expanded at right angles to the incident rays as in *a*. The chromatophores change their positions only with a change in the direction or the intensity of the illumination, but under favorable conditions the changes can be accomplished rapidly.

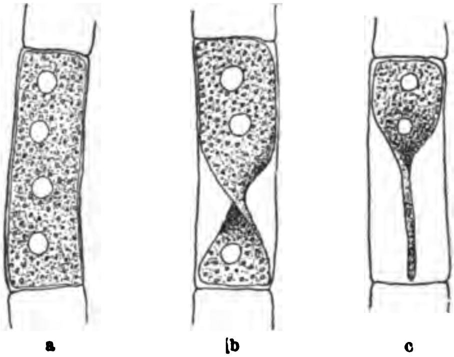

Figure 18. Cells of *Mesocarpus Sp.*
a—cell with chromatophore in diffuse daylight position.
b—chromatophore bending in too intense light.
c—chromatophore bent to reduce absorption of light.

Whether heliotropism and heliotaxis are or are not fundamentally similar phenomena there is no experimental evidence for determining. The effect of light upon the cell is not precisely known, though it is probable that it chemically affects substances contained in the cell, and that the changes in these stimulate the protoplasm (see p. 210). The protoplasm of one or more cell-members of a tissue may react by changing the form, size, turgor, or some other quality of the cells, thus causing a change in the form or direction of an organ (heliotropism). This change may be made permanent by growth without being directly accomplished by growth. The same change in form, size, turgor, or other quality of isolated cells may result in locomotion (heliotaxis). In both instances the effect of light might be intrinsically the same, the reaction of the protoplasm to chemical stimulation also the same, the result being different only because one cell could move freely while the other was obliged to move more than itself.*

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* Oltmanns. F. l. c., p. 209.

INFLUENCE OF HEAT

The degree of heat prevailing in the medium—air, water, soil—in which a plant is growing, and the radiant heat falling upon the plant and its immediate surroundings, exert definite influences upon its activities. Without its minimum degree of warmth, the plant will survive only in a resting condition, if at all. There is also a maximum temperature which can be withstood only in the resting condition. Apparently there is no temperature so low as to be fatal to resting protoplasm—seeds, spores, etc.—and the maximum for dry resting protoplasm is surprisingly high. There are, however, minimum, optimum, and maximum temperatures for active protoplasm, which are definite and definitely related to each other. Organisms living where the mean temperature is low have low minimum and maximum temperatures. The native plants of warm situations have correspondingly high extreme temperatures, and plants accustomed to living where there is only slight variation in temperature can be cultivated only under similar conditions. These statements are illustrated by the following table:*

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* Loeb, J. Zur Theorie der physiologischen Licht und Schwerkraftwirkungen. Archiv f. d. gesam. Physiologie, Bd. 66, 1897. Einleitung in die vergleichende Gehirnphysiologie und vergleichende Psychologie. Leipzig, 1899.

	min.	opt.	max.
Hydrurus fœtidus	0°	10°	below 16°
Ulothrix zonata	C°	below 15°	24°
Zea mais	9°	34°	46°
Cucurbita pepo	14°	34°	46°
Bacillus thermophilus	42°	63-70°	72°
" tuberculosis	30°	38°	41°

It is greatly to be regretted that those organisms which apparently transgress the general laws expressing the relations of active protoplasm to heat have been so little studied by physiologists. The vegetation of geysers and hot-springs, and of the very cold waters from glaciers and persistent snow-deposits, has been studied too exclusively by systematists. The temperatures of the waters are known only in a general way, the temperature of the water actually bathing the organisms and the exact condition of the organisms have not been accurately determined.† Each actively fermenting manure-heap, each mass of organic matter so rapidly decomposing that high temperatures develop in it (*e.g.* where hay "heats" in cock or mow), is the seat of bacteria, the optimum temperatures of which are above the maxima for most forms. The difficulty of successfully imitating the natural conditions hampers experimental study of these organisms.

Continental bodies of land are subject to considerably wider extremes of temperature than prevail in oceanic islands and in certain limited and peculiarly situated areas near the coast. These show limited ranges of temperature, but it is possible to cultivate there plants which naturally occur much farther north or south. This is partly the reason why semi-tropical and decidedly northern plants can be successfully cultivated in the region about the Bay of San

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* See Pfeffer's Pflanzenphysiologie, Bd. II., p. 87, 1901.

† Davis, B. M. Vegetation of the hot-springs of the Yellowstone Park. Science. VI., 1897. Tilden, J. E. Observations on some West American thermal algæ. Bot. Gaz., vol. 25, 1898.

Francisco, in California, for there the respective minimum and maximum temperatures of these forms are never attained. The optimum temperatures for most plants in this region are maintained for only very short times, owing to the great daily range in temperature, but are frequently repeated, owing to the slight seasonal ranges. The frequent occurrence of optimum temperatures may more than compensate for their brief duration—a matter, however, which requires proof.

Movements and locomotion, as well as the rate of growth, are more or less controlled by heat. *Thermotropism* and *thermotaxis* are the irritable responses to the stimulus of heat. A certain degree of warmth will induce positive thermotropism or thermotaxis—respectively, growth and locomotion towards the source of heat—while a higher or lower degree of heat may induce the opposite, negative thermotropism or thermotaxis. Roots, for instance, grow toward but not into contact with steam or hot-water pipes passing through the soil between buildings. Roots of Indian Corn* will grow toward the source of heat till they reach a point where the temperature is 37.5° C. They will bend and grow away from any warmer part of the soil. Ordinarily in nature, however, thermotropic sensitiveness is of little advantage to the plant. There is no differentiation into sensory and motor zones, the whole growing region being equally sensitive. A certain degree of warmth is required in order that the organism may be sensitive to other influences. Thus heat must arouse the parasitic dodder (*Cuscuta*) to a certain degree of sensitiveness else it will not be able to respond to the contact stimulus (see pp. 244–5) upon which its attachment to the host absolutely depends.†

The sensitiveness and the response of motile organisms to heat is manifestly important. The sensitiveness to heat

The organs especially active in absorbing nutrient aqueous which causes a man who is cold to approach the fire but not to draw too close, and when warmed to move to a slightly cooler spot, is not peculiar to him or to higher animals. This example of thermotaxis expresses the sensitiveness of all living protoplasm and the habit of all motile organisms to seek positions which are most comfortable because most favorable to the accomplishment of their vital functions. Thus slime-moulds* and zoospores† are known to move toward sources of heat.

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* Wortmann, J. Über den Einfluss der strahlenden Wärme auf wachsende Pflanzentheile. Bot. Zeitung, 1883. Über den Thermotropismus der Wurzel. Bot. Zeitung, 1885.

† Peirce, G. J. A contribution to the physiology of the Genus Cuscuta. Annals of Bot., Vol. VIII., 1894.

Whether, corresponding with the influence of light, the direction of movement of the internal organs of the cell is affected by the direction of the source of heat seems not to have been studied. The rate of movement of the organs of the cell in relation to the degree of warmth has been carefully examined. For example, the chlorophyll grains in *Elodea*, *Valisneria*, and *Chara* circulate with increasing rapidity up to a temperature of 34 to 38° C., but at 44° all movement ceases, though it will be resumed when the temperature is lowered.‡ The temperature at which the protoplasm circulates most rapidly in these plants is near the optimum for most of the activities of the cell.

INFLUENCE OF WATER

A sufficient quantity of water is a necessary condition for active life (p. 6). Water is also an essential component of the living structure, protoplasm (p. 7). Given the minimum amount of water for the erection of the living structure after a period of inaction, the organism will resume its functions. The germination of seeds and spores shows this. Increase in the amount of water from the minimum to the optimum is followed by increase in all the vital activities. This is consistent with chemical and physical experience in the laboratory, a minimum quantity of water being indispensable to many reactions, a larger(optimum) amount causing them to take place more rapidly or more energetically. There are, therefore, minimal and optimal quantities for the physical states and the chemical processes in the living cell and the living organism, but until water is sufficient in amount to become the vehicle of mechanical forces, there cannot be said to be any maximum quantity. The minimum and optimum vary with the organism.

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* Stahl, E. Zur Biologie der Myxomyceten. Bot. Zeitung, 1884.

† Strasburger, E. Wirkung des Lichtes und der Wärme auf Schwärmsporen. Jenaischer Zeitschrift, 1878.

‡ Velten, W. Einwirkung der Temperatur auf die Protoplasmabewegung. Flora, 1876.

An organism will absorb water up to a given amount, but it can absorb no more (see p. 110) because the substances which it contains do not offer the physical conditions making further absorption possible. The absorption of water gives rise to changes in the physical conditions prevailing within the cells (pp. 210–11), the changes manifesting themselves most conspicuously in an increase in volume or pressure, or both. These physical changes directly affect the living protoplasm. The greater pressure or larger volume of individual cells enables them to exert greater mechanical force upon their surroundings and to occupy more space; it enables the organ which they compose to expand or to come into a more favorable position, etc. Besides these mechanical effects of water, which influence the living protoplasm, the greater or less quantity of water in the cell exercises a direct physiological effect upon the activities of the cell. When the plant or the cell needs water, its activities will be reduced, within certain limits, in proportion. Conversely, any increase, under these conditions, in the amount of water available will stimulate the plant or the cell.

Water exerts two distinct influences upon the plant. This can best be shown by examining the directive influence of water upon growth. First, let the downward-growing primary root of a seedling growing in air not excessively damp be exactly measured as to diameter and length by the eyepiece micrometer of a horizontal microscope; then plunge this root into water of the same temperature as the air and note the increase in dimensions which promptly follows. This is a purely mechanical effect, swelling. Again, let seedlings be grown in any apparatus which will expose the roots to unequal amounts of moisture on opposite sides; for instance, Sachs's familiar cylinder of wire-netting filled with damp moss or moist earth.* If this cylinder be hung slanting at an angle of about 45°, the roots will not grow vertically downward away from the cylinder, but will follow along its under side in spite of the geotropic stimulus (p. 204). In this experiment the roots bend in the direction from which they obtain water. In the first experiment the absorption of water is followed by expansion, swelling. In the second experiment that side expands which is not able directly to absorb water, while that side which does absorb water does not expand as much. In the first experiment the physical influence is uniform on all sides of the root, which swells uniformly. In the second experiment, the physical influence was greater on one side than on the other, the tendency to swell on one side was offset by the increased activity of the protoplasm, the more rapid growth, of the opposite side, in response to stimulus. Such a reaction as this is called *hydrotropism.*

The hyphæ of *Mucor* grown on moist bread over water are deflected when they reach the surface of the water, growing instead horizontally over it and against the bread. This bending away from water is not negative hydrotropism, but rather the reaction of the hyphæ to other stimuli such as food, oxygen, etc., which are more abundant in the bread than in the water.

Sachs's experiment (see above), with roots deflected by moisture from the vertical position, reveals a very important principle. It is manifestly more important for the root as an absorbing organ to grow where it will obtain needed aqueous solutions than for it to be in any particular position with relation to the vertical; but in order that the older parts of the root may give the needed mechanical support to the plant, the root must grow downward into the soil. There must therefore be a delicate balance in the sensitiveness and the reactions to geotropic and hydrotropic stimuli.

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* Sachs, J. von. Über die Ablenkung der Wurzeln von ihrer normalen Wachsthumsrichtung durch feuchte Körper (Hydrotropismus). Arb. d. bot. Inst. Würzburg, Bd. I., 1871–4. Gesam. Abhandl., Bd. II., 1893.

solutions—roots, rhizoids,* pollen-tubes,† etc.—are the ones most sensitive to differences in the proportions of water in their environment. Other organs are relatively or quite indifferent. Most stems are not hydrotropically sensitive, but the peculiar stem of the parasite, dodder (*Cuscuta*), which must twine closely about living plants and extract nourishment from them, is somewhat sensitive.‡

The size and number of root-hairs is inversely proportional to the ease with which the plant obtains the water it needs. The difficulty of absorbing water in sufficient quantity to meet the demand made by transpiration and evaporation (see p. 141) from the aerial parts acts as the stimulus to the young epidermal cells of the root to grow larger and into such form that they will be able more readily to absorb the water held on the surfaces of the soil particles. An amount of water in the soil less than the optimum is followed by elongation of the epidermal cells, and they grow out as hairs. Seeds germinated in moist air instead of in damp soil develop a larger number of still longer hairs. On the other hand, the roots of seedlings growing in water are nearly or quite bare of hairs. The stimulus to the production of root-hairs may develop within the plant itself. It may consist in the osmotic withdrawal of water from the epidermal cells to make good the losses above. In any case, water exerts the stimulus to growth, and the living protoplasm reacts to the stimulus.

The root-hairs grow toward and around soil particles. These hold films of water on the surface. The growth of the root-hairs toward the soil particles is evidently positively hydrotropic. The growth of the hairs around the particles may be the combined result of the stimulus of contact with the solid (see p. 241) and of water.

The opposite result, the growth of parts away from water, is shown by the sporangiophores of some of the fungi. It may well be that the fruiting organs of other plants dependent upon dry air for the best dispersal of their seeds or spores are also negatively hydrotropic.*

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* Molisch, H. Untersuchungen über den Hydrotropismus. Sitzb. d. K. K. Akad. der Wiss., Wien, 1884.

† Miyoshi, M. Über Reizbewegung der Pollenschläuche. Flora, Bd. 78, 1894.

‡ Peirce, G. J. Contribution to the physiology of the Genus Cuscuta. Annals of Botany, vol. VIII., 1894.

Hydrotaxis is exhibited by many of the slime-moulds, for example *Æthalium* (*Fulligo*). Stahl† shows that the distribution of these plants on and in the rotting wood, etc. where they live, corresponds to the distribution of water there; they are positively hydrotactic.

The locomotion of such plants as are motile at any time is dependent upon water, for this is the only medium through which they can propel themselves. Many other movements than those of locomotion are also dependent upon water; the withdrawal of water, or variation in the amount of water, may cause purely physical changes in cell-walls or dead tissues which result in the exercise of mechanical force. These *hygroscopic* movements, such as the opening of the peristome in mosses, the action of the elaters of liverworts and *Equisetum*, the opening of fern-sporangia, the curling of the awns of Geraniaceæ, the splitting open of pods, etc., etc., are free from the action of living protoplasm, and are mentioned in connection with irritable phenomena only to make the difference clear.

INFLUENCE OF OTHER SUBSTANCES THAN WATER

In the whole range of chemical substances there are extremely few which never in any way affect living protoplasm. Many substances, however, affect protoplasm only mechanically—as obstacles in the way of its growth or movement, or, like the nitrogen of the air, which blows against and subjects it to strain, etc. (For the effects of these see p. 189). Unless a substance is soluble in water it can affect protoplasm in no other than mechanical ways. Of the soluble substances some affect protoplasm favorably, others unfavorably, others not at all. When an effect is produced, it may be purely physical or it may be chemical, involving some change in composition. The same substance in different concentrations, may produce favorable or unfavorable effects or apparently none, and the effects may be first physical and then chemical, or *vice versa*. The effect produced is dependent upon, 1st, the acting substance, 2d, the organism, 3d, the conditions prevailing at the time. The organism will vary at different times in its activities, contents, and composition, and will therefore vary in its reaction or response to external influences.

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* Preliminary experiments on *Fimbriaria California* lead me to believe that the sporophyte of this and of other liverworts (*e. g. Anthoceros*) may be negatively hydrotropic.

† Stahl, E. Zur Biologie der Myxomyceten. Bot. Zeitung, 1884.

In studying the influence of gravity upon plants, we were dealing with a constant force and a varying organism. In studying the influence of light, we were dealing with a varying force as well as varying organism, but the force produces its effects always by the same means. In studying the influence of water, we were dealing with a single, simple compound varying in quantity, but in its effects only because of this fact and of the varying organism. In studying the influence of other substances upon protoplasm we have to deal with their relations to water and to each other as well as to the organism. This materially complicates the subject. The effects of common salt illustrate these several points. A very dilute solution of common salt ($NaCl$) acts unfavorably upon plants the roots of which are bathed in it. The sodium and chlorine atoms become dissociated and act as independent poisons. Whether the poisonous action of these atoms is due to their own chemical properties or to their electrical charges is not certain and at all events need not now be discussed.* A solution of such concentration that the atoms are not dissociated and that molecules remain intact will have no effect. Still further concentration will cause plasmolysis of the living cells.

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* Kahlenberg, L., and True, R. H. On the toxic action of dissolved salts and their electrolytic dissociation. Bot. Gazette, XXII., 1896. True, R. H. The physiological action of certain plasmolyzing agents. Bot. Gazette, XXVI., 1898. Heald, F. D. On the toxic effect of dilute solutions of acids and salts upon plants. Bot. Gazette, XXII., 1896. Loeb, J. On ion-proteid compounds and their rôle in the mechanics of life-phenomena. I. The poisonous character of a pure NaCl solution. Amer. Journ. Physiol., vol. III., 1899-1900.

This in itself is injurious, though the cells may recover their turgor, becoming adjusted to the greater density. Plants continually exposed in nature to salt solutions of considerable density present a very different appearance from those growing under more usual conditions.* They are usually fleshier and coarser, often more compact in habit, than ordinary land plants (compare *Solidago sempervirens* with the other *Solidagos* of New England, the marsh grasses with those of meadows, etc.).

The theory of electrolytic dissociation of the atoms of substances dissolved in proportionally large volumes of water is extremely useful to the physicist and chemist. It has been profitably employed by some physiologists in discussing the poisonous effects of certain substances ordinarily harmless. The theory is useful, but it is very far from experimental proof. Nevertheless it may be employed in plant physiology to suggest possible explanations of otherwise incomprehensible phenomena. We may conceive the cell-sap —an aqueous solution of a great number of substances in very various and inconstant amounts—as containing not only substances still in the molecular state, but also substances in a state of atomic dissociation, in which the component atoms are scattered at considerable distances from each other throughout the solution. Whether these dissociated atoms or groups of atoms smaller than molecules are charged with electricity—some positive, others negative—or whether the atoms possess only their chemical properties and affinities is by no means known. Certain it is, however, if there are dissociated atoms in the cell-sap, that these atoms are more susceptible to physical and chemical influences within and without the cell, and more prompt and active in response, than are atoms associated in molecules. Dissociated atoms exhibit the properties of the chemical elements, whereas associated atoms present only the properties of compounds. The elements are more ready for combination than compounds are for recombination. A dilute solution, one containing dissociated atoms, is therefore more sensitive to external influences and is more likely to change than is a concentrated solution. Some of the substances in the cell-sap may be present in such minute quantities as to be dissociated. In this case these dissociated atoms, and in consequence the cell-sap as a whole, would be very sensitive to external influences, physical and chemical. Anything influencing the cell-sap in any way immediately affects the protoplasm through the cell-sap which permeates every part of it. This influence upon the protoplasm may be chemical or it may be electrical. Only the future can decide which it is, but meantime this conception assists us in appreciating how the protoplasm may be affected and how the stimulus may be promptly transmitted from cell to cell.*

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* Schimper, A. F. W. Pflanzengeographie auf physiologischer Grundlage. Jena, 1898.

Any substance or any force which disturbs the balance between the constructive and destructive processes maintained by the organism or the cell will affect the organism, producing an irritation equal to the disturbance. If the new balance necessitated by the introduction of the new substance or the new force is more or less favorable to the accomplishment of the vital processes than the old, the living cell or organism will respond accordingly. Organisms living in certain situations are exposed to very frequent and very rapid changes in their environment. Thus the plants living between the high and low tide marks on the seacoast are subjected to a twice daily change in their relations to water. If rain falls upon them while they are bared by the tide, they are subjected to still another change. Marine plants living at the mouths of fresh-water streams are also exposed to frequently repeated and very rapid changes in the composition and density of the medium which surrounds them. Such changes in osmotic influences imply a very great range of adaptability on the part of the plants regularly exposed to them. Plants living in situations where osmotic influences change only gradually or slightly, as in pools which dry up during the summer, or in bodies of water which are added to only occasionally or seasonally, are far more susceptible to changes in the density of the water. It has been suggested that the recourse of fresh water algæ to their various modes of reproduction (see pp. 268–9) may be a reaction to osmotic differences in the water in which they live,* but this is by no means assured.

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* Matthews. A. P. The nature of the nerve impulse. Century Magazine, vol. 63, 1902. Abstract also in Science, vol. 15, p. 344, 1902.

Certain substances, nutritious and other, stimulate the growth and other activities of plants as of animals. Small amounts of poisonous matters, such as ether,† metallic salts, cocaine, and morphine‡ act as stimulants. The principle governing the action of these substances is the same as that controlling the use of tea, coffee, and tobacco by human beings, for all of these drugs are dangerously depressing poisons when taken in concentrated form. Alcohol may, in both animals and plants, serve as a source of energy by oxidation and thereby stimulate the organism.§

One word must be said about the startling claim that definite chemical stimuli may replace the male elements in sexual reproduction. Loeb §§ reports that he has reared sea-urchins through the earlier larval stages from unfertilized eggs by subjecting the eggs to suitable chemical stimuli. From this he argues that the main function of the sperm is to supply the eggs with certain compounds indispensable to further development, and that when, no matter by what means, these compounds are supplied, development will go on. This may be true, but that it is true is far from proved. There are well-known cases of parthenogenesis among both animals and plants. From these one might infer either that no eggs require fertilization in order to develop, or that these eggs are chemically stimulated to develop by the substances in air or water. Both of these inferences would be unjustified. Sea-urchin eggs may not develop parthenogenetically when let alone, though they may do so when chemically stimulated. But it is a far cry from Loeb's brilliant experiments to the generalization that fertilization is principally chemical stimulation. In many cases, the structure of the egg must be completed by the material of the sperm before normal development can begin. This, in a sense, is chemical stimulation, but it is also a morphological process. Fertilization, in most cases at least, consists in the completion of the structure of the egg as well as in the stimulation of its living protoplasm to grow, etc.

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* Livingston, B. E. Nature of the stimulus which causes change of form in polymorphic algæ, Bot. Gazette, vol. 30, 1900. Further notes on the physiology of polymorphism in green algæ. Bot. Gazette, vol. 32, 1901.

† Townsend, C. O. The correlation of growth under the influence of injuries. Annals of Bot., XI., 1897.

‡ Richards, H. M. Die Beeinflussung des Wachsthums einiger Pilze durch chemische Reize. Jahrb. f. wiss. Bot., Bd. 30, 1897. See also Raciborski, M. Über den Einfluss äusserer Bedingungen auf die Wachsthumsweise des Basidiobolus ranarum. Flora, Bd. 83, 1896.

§ Atwater, W. O. Metabolism of matter and energy in the human body. Bull. U. S. Dept. Agriculture, Washington, 1901.

§§ Loeb, J. On the nature of the process of fertilization and the artificial production of normal larvæ (plutei) from the unfertilized eggs of the sea-urchin. On the artificial production of normal larvæ from the unfertilized eggs of the sea-urchin (Arbacia), Amer. Journ. Physiol., vol. III., 1899-1900.

The direction of growth, as well as the rate and kind, is influenced by other substances than water. This response of the living plant to external stimuli is called *chemotropism.* It is well known that roots grow toward, around, and into especially fertile clods of earth, leaving the less nutritious. The distribution of oxygen, carbon-dioxide, and possibly of other gases in the soil (*e. g.* illuminating gas leaking from underground pipes) affects the growth of the roots.* They will not grow far down into water; they will turn up whenever their supply of air falls below the optimum. They will grow toward the sources of many gases, but so soon as they reach a point where the amount of gas becomes at all considerable, they will bend and grow away.

The chemotropic sensitiveness of hyphæ † and of pollen-tubes ‡ is marked and important. Miyoshi finds that the spores of various fungi, germinated on finely perforated films of collodion or of stomata-bearing epidermis floating on water or solutions of various substances, or on the stomata-bearing surface of *Tradescantia* leaves injected under the air-pump with solutions of the substances to be tested, send out hyphæ which grow toward and through the perforations into the solution, or away from the perforations, according as the substances used are attractive or repellent. The attractive substances are not all nutritious, the repellent not all poisonous. Osmotic and dissociation phenomena may be concerned. Glycerine and gum arabic, nutritious though they are, do not attract. Miyoshi and Lidforss report that the direction of growth of pollen-tubes is influenced by water, oxygen, sugars, and easily diffusible proteids, especially those composing and associated with enzyms. All of these are present in various amounts in the different parts of stigma, style, and ovary. Lidforss says that the direct growth of the pollen-tube toward the micropyle is due solely to hunger—certainly a graphic expression. On scattering various kinds of pollen and the spores of *Mucor* with ovules of *Scilla* on moist agar-agar, Miyoshi found *Mucor* hyphæ and pollen-tubes growing toward and even into the ovules.

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* Molisch, H. Über die Ablenkung der Wurzeln von ihrer normalen Wachsthumsrichtung durch Gase (Aërotropismus). Sitzb. d. Akad. d. Wiss., Wien. Bd. 91. I., 1884.

† Miyoshi, M. Über Chemotropismus der Pilze. Bot. Zeitung, 1894.

‡ Miyoshi, M. Über Reizbewegungen der Pollenschläuche. Flora, Bd. 78, 1894. Lidforss, B. Über den Chemotropismus der Pollenschläuche. Ber. d. Deutsch. Bot. Ges., Bd. 17, 1899.

The meeting of the conjugation tubes of *Spirogyra* cells could hardly occur with such regularity if it were merely a matter of chance. On the other hand, experimental proof that their growth toward one another is chemotropically directed is so difficult that no attempts have yet succeeded. It has been noticed* that bacteria are attracted to those portions of *Spirogyra* cells which grow out into tubes. From this it is inferred that some special substance diffuses from the tubes. This substance may not induce the cell in an adjacent filament to put out a tube, yet it may so direct the growth of a tube already forming that the two will meet. Too much reliance should not be placed on inference from such evidence, however, for though the behavior of bacteria where only one kind is concerned may be definitely known, the behavior of a swarm of several or many kinds is due partly to the influence of the bacteria themselves upon each other.

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* Overton, C. E. Über den Conjugationsvorgang bei Spirogyra. Ber. d. Deutsch. Bot. Ges., VI., 1888. Haberlandt. G. Zur Kenntniss der Conjugation bei Spirogyra. Sitzb. d. K. Akad. d. Wiss., Wien, Bd. 99, I. 1890.

One of the most striking responses to chemical irritation is that exhibited by the tentacles on the leaves of the various species of the carnivorous Sundew, *Drosera*. The thorough investigation of this by Darwin* has placed our knowledge on a very definite basis. He found that the tentacles would bend over and the leaves curl with a promptness and to a degree proportional to the irritating quality of the substance used. That it was not mere contact that caused the irritation was experimentally demonstrated by placing bits of wood, quartz, etc., and drops of milk, beef infusion, etc., upon the tentacles of expanded leaves. The wood, quartz, etc., did not induce the tentacles to close over them; the drops of nutrient liquid did. Darwin then tested the influence of a great variety of substances and found that some did, others did not, stimulate the tentacles to close over them.

The effects of fragrant substances in directing the locomotion of animals is a fact of such universal experience that we may well use it as the starting-point of our discussion of *chemotaxis*. Flies are attracted by the odors of cooking and repelled, as every camper knows, by a smoky fire. Walking, crawling, and swimming animals are attracted or repelled by soluble substances, either in the solid form or in solution. Ants will follow a trail of grains of sugar to its source, but they will be turned from their path by unpleasant substances placed in their way.† Insects, and doubtless birds also, concerned in the cross-pollination of flowers, are attracted from a distance by the odorous substances formed in them. Only when the animal comes near enough for the flower to be within its range of vision is it attracted by the distinguishing color and form. The direction of locomotion by taste and scent is but the special form of chemotaxis exhibited by higher animals. In the lower animals and in plants, in which the separate senses are not seated in specially differentiated organs, the same sensitiveness of the living protoplasm is exhibited, in a degree not always less striking.

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* Darwin, C. Insectivorous Plants. On cytological changes in gland cells following stimulation see Huie, L. H., in Quart. Journ. Microsc. Sci., vols. 39 and 42, 1896 and 1899; and Rosenberg, O., Physiolog.-cytolog. Untersuch. über Drosera rotundifolia. Upsala, 1899.

† Lubbock, Sir John. Ants, Bees, and Wasps. New York, 1884.

The habit of motile aërobic bacteria of gathering around air-bubbles and at the edges of the coverglass in microscopic preparations is of common observation. Correspondingly, in preparations made without air-bubbles and cut off from a supply of air by sealing the margins with vaseline, the bacteria become uniformly distributed and presently come to rest. This indicates the dependence of such bacteria upon oxygen as a source of energy. Their uniform distribution when the supply of oxygen is uniform, and their collecting around the greater quantities when the supply is scattered irregularly, indicate the importance of oxygen in directing as well as maintaining their movements. The chemotactic movement of certain bacteria in relation to oxygen was carefully studied by Engelmann* and made use of by him in determining which of the component rays of sunlight are most efficient in the manufacture of food by the chlorophyll grain (see p. 56). By placing a filamentous alga under the coverglass with the bacteria, and duly illuminating the preparation, the alga will become photosynthetically active and liberate oxygen, the bacteria gathering about it. If a short spectrum, instead of white light, be thrown on the alga, the cells exposed to the yellow light will give out most oxygen, as shown by the largest number of bacteria collecting there.

The chemotactic movements of bacteria with relation to conjugating *Spirogyra* filaments have already been referred to (p. 232). Bacteria are known to collect on the surface of decaying matters, attracted thither by the substances diffusing from the dead organic material. The sensitiveness of the bacteria of disease to the dissolved substances in the body of their host enables them to move toward and into the places most favorable to them. The chemotactic sensitiveness of bacteria, flagellates, *Volvocineæ*, and motile reproductive bodies was studied very thoroughly by Pfeffer.* His method consisted in the employment of capillary tubes closed at one end and partly filled under the air-pump with solutions of the substances to be tested. These tubes, after rinsing, he introduced into drop-cultures or under the coverglass on the slide. From the mouths of such tubes the molecules of the dissolved substances diffuse in all directions into the surrounding liquid and presently impinge upon the motile organisms present. Such impinging molecules set up an irritation within the cell. When this irritation is sufficient, the organism reacts by changing its position, moving so that its long axis becomes parallel to the line of advancing molecules, and presently going either toward or away from the source of the irritating substance, according as this substance attracts or repels. Pfeffer found that certain substances attract, others repel, and still others induce no change in the direction of locomotion. Pfeffer's list has been considerably lengthened by one of his pupils, Buller, who worked on the antherozoids of ferns.† As a result of Pfeffer's work it is now generally accepted that the antherozoids of ferns, liverworts, and algæ make their way to the egg-cells under the definite attraction of soluble substances diffusing from the egg-cells themselves, or from a part or the whole of the oögonium or archegonium. The specifically attractive substances are unknown, though it is inferred in the case of ferns that malic acid is the attractive agent, and cane-sugar in the liverworts. This inference is based on experience only to this extent: malic acid is present in fern prothalli bearing sexual organs, and capillary tubes containing a 0.05% solution of malic acid collected one hundred fern antherozoids in an hour from a drop of water in which there were many. The evidence for cane-sugar is similar. Presumably the free egg-cells of *Fucus*, etc., are fertilized by chemotactically attracted antherozoids, but proof of this is wholly lacking. Much physiological work of this kind remains to be done on the reproduction of the fresh and salt water algæ.

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* Engelmann, T. W. Eine neue Methode zur Untersuchung der Sauerstoffausscheidung pflanzlicher und thierischer Organismen. Archiv. f. d. ges. Physiol., Bd. 25, 1881. L'émission d'oxygène sous l'influence de la lumière par les cellules à chromophylle, demonstrés au moyen de la méthode bactérienne. Archives Néerland., T. 28, 1894.

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* Pfeffer, W. Locomotorische Richtungsbewegungen durch chemische Reize. Unters. a. d. bot. Inst. z. Tübingen, Bd. I., 1884. Über chemotaktische Bewegungen von Bakterien, Flagellaten und Volvocineen. *ibid.* Bd. II., 1888. *See also* Jennings and Crosby on manner in which bacteria react to stimuli, especially to chemical stimuli. Amer. Journ. Physiol., vol. VI., 1901.

† Buller, A. H. R. Contributions to our knowledge of the physiology of the spermatozoa of ferns. Annals of Botany vol. 14, 1900.

Pfeffer's work on chemotaxis was quantitative as well as qualitative. He showed that Weber's law, that "the smallest change in the magnitude of a stimulus which will call forth a response always bears the same proportion to the whole stimulus," applies to chemotactic as to other stimuli. In the case of "*Bacterium termo*"—now known to be a mixture of several species of short rod-shaped bacteria—Pfeffer found, in the first place, that there must be more of the attractive substance in the capillary than outside, and then that if the hanging-drop culture contain 0.01% meat extract, the bacteria will not swim toward and into a capillary containing less than 0.03% and that they are attracted more and more strongly by solutions containing 0.05%, 0.08%, and 0.1%. The same organisms in a culture containing 0.1% meat extract will be attracted only by capillaries containing 0.3%, 0.5%, 0.8%, and 1.0% solutions of meat extract. Similarly, the bacteria are drawn from a 1% solution only by a 3% solution or stronger. We see then that the attractive substance must be increased by stages of three in order that there may be a change in the direction of locomotion. This does not imply that there is no stimulation with less, for there may well be, only that there will not be a response in the form of a change in direction of locomotion. In order to induce an organism in an environment of a certain degree of favorability to leave this for another, there must be a decidedly larger proportion of the stimulating substance.

Chemotropism and chemotaxis may be due to fundamentally the same causes, though there is no proof of this. (See discussion of heliotropism and heliotaxis on page 219.) If the chemical theory advanced in explanation of the influence of light upon the direction of growth and of locomotion be true (p. 210), the influence of light upon the living protoplasm is only through those compounds in the cell which are acted upon by light. So far, then, as the protoplasm only is concerned, it may be that heliotropic and heliotactic phenomena are intrinsically chemotropic and chemotactic. The sources of the influence upon the chemical compounds within the cell are different, the influence which directly affects the living protoplasm may be only that of chemical compounds, not of light.

INFLUENCE OF ELECTRICITY

The electrical conditions in soil and air are constantly changing, but except at rare intervals no great amount of electrical force becomes evident or is concentrated in any one place. Under natural conditions living organisms are ordinarily exposed to feeble currents only, and to such they are accustomed. Under the artificial conditions prevailing in the planted streets and in the parks of cities, in the soil of which powerful electric currents are induced or through which they are transmitted in consequence of the very general use of electricity, the roots of plants are periodically or constantly subjected to more violent electrical influence. Not all electricity, however, comes from without, for in the plant itself, under normal conditions, electrical as well as other currents are constantly developed and maintained. These are very likely due to the chemical changes going on in the plant and in its different parts, and just as these processes affect the balance of other forces—of heat, osmosis, and chemical energy—so they may readily alter the balance of electrical tensions in different parts of the organism and thereby set up electrical currents. If, by chemical and physical changes in the organism, electrical currents develop in it, it is natural to suppose that electrical influences brought to bear upon the organism from without will effect chemical and physical changes within it. These changes, whether in the living protoplasm itself or in its lifeless contents, cannot be without influence upon the protoplasm itself.

According to Loeb*—"probably all electrical effects on living things are only indirect. What we call electrical effects are really due only to the chemical and molecular action of the ions or the compounds formed from these" set free in the living cells, or in the living organism, by electrical force. Such an hypothesis as this is certainly comprehensive enough. Protoplasmic tensions and the strength of the protoplasmic structure would surely vary with the chemical and physical rearrangements taking place in the dissolved salts of the cell-sap throughout the living cell.

In spite of considerable experimental study of the possible influence of electricity upon the rate and amount of growth no general statement regarding it is now possible. Some authors† claim that plants screened from atmospheric electricity are smaller than plants grown under otherwise similar conditions. Others‡ assert that increasing the atmospheric electricity by discharges from wires strung above the plants, increases both the growth and the yield. The eminent German agricultural physicist, Wollny,§ having critically re-examined the subject, denies both claims. We may, therefore, safely leave this question to the sanguine students of applied botany, only hoping that the farmer will not be led to cumber the ground and mar the landscape with unsightly screens of telegraph wire.

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* Loeb, J. Zur Theorie des Galvanotropismus. Archiv. f. d. ges. Physiologie, Bd. 67, 1897.

† Grandeau, L. De l'influence de l'électricité atmosphérique sur la nutrition des végétaux. Ann. de Chem. et de Physique., T. XVI., 1879. Aloi, A. Dell' influenza dell' elettricità atmospherica sulla vegetazione delle piante. Bull. Soc. Bot. Italiana, 1895.

‡ Lemström, S. Om elektricitens inflytande på växterna. Helsingfors. 1890. Abstract by Bailey in Trans. Mass. Hortic. Soc., 1894. *Also* Electricultur. Erhöhung der Ernteerträge aller Culturpflanzen durch elektrische Behandlung. Übers. von Pringsheim. Berlin, 1902.

§ Wollny, E. Elektrische Culturversuche. Forsch. a. d. Gebiete d. Agrik.-Physik., Bd. XVI., 1893.

The net result of the many attempts to hasten the germination or to increase the germinating-power of seeds by subjecting them to electrical action seems to be that there are such great differences between plants of different species that no general rule can be formulated.* Experiments on the possible effects of the X or Röntgen rays upon the growth of plants, from the pathogenic bacteria up, have led mainly to negative results.

It is claimed that the direction of growth is influenced by electrical currents, that plants are galvanotropic or electrotropic, positively or negatively, at least as to their roots.† If Loeb's hypothesis (p. 238) be true that electrical currents set up chemical changes in the cell, it would be surprising if these produced no effect as shown by the direction of growth. Still, the subject is far from exhausted.

Electrotaxis in plants is almost uninvestigated. Some work on the movements of bacteria ‡ with relation to electrical currents has been done, but with meagre results. Zoospores would suggest themselves as favorable objects of study.

INFLUENCE OF CONTACT

By the term *contact* is implied much the same idea as is expressed in the physiology of higher animals and in common parlance by the word *touch*. When the human finger gently touches a motionless clean glass rod, the temperature and other physical properties of which are similar to those of adjacent objects, the mind is conscious of the contact. Solid object and solid object exert on one another certain influences. The finger imparts a certain amount of warmth, of moisture perhaps, possibly of other forces and substances, to the rod, and the rod also acts upon the finger. The contact of solid objects with plants and plant-parts enables them directly to influence each other. Only when the plant or plant-part is more responsive than the lifeless object, only where there is a visible reaction to the influence thus exerted, can we tell either the character or the extent of the influence. By studying the reactions to the influence exerted by contact we can divine something regarding the nature of the stimulus.

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* For description of method and the detail of beneficial effects of electrical stimulation see Kinney, Electro-germination. Bull. Hatch Experimental Station, Amherst, Mass., Jan., 1897, and Stone, Influence of Electricity on plants. Bot. Gazette, vol. 27, 1899.

† Elfving, F. Über eine Wirkung des galvanischen Stroms auf wachsende Keimlinge. Botan. Zeitung, Bd. 40, 1882. Brunchorts, J. Über Galvanotropismus. Ber. d. Deutsch. Bot. Ges., Bd. II., 1884, and Bot. Centralbl., Bd. XXIII., 1885.

‡ Verworn, M. Die polare Erregung der Protisten durch den galvanischen Strom. Arch. f. d. ges. Physiol., Bd. 46, 1890, p. 291. Lortet, L. L'influence des courants induits sur l'orientation des Bactéries vivantes. Comptes Rendus de l'Acad. des Sciences Nat., Paris, T. CXXII., 1896.

When zoospores and other motile and floating spores of sessile plants come to rest, attaching themselves to the substratum, the attachment is effected through means not yet wholly clear. The course of events is briefly this. When a spore, *e. g.* of *Vaucheria*, *Œdogonium*, *Fucus*, etc., comes to rest against the surface of a solid object—a dead leaf or branch or stone—its form changes and the naked mass of protoplasm invests itself with a cell-wall. The part of the cell against the solid object flattens, spreads out somewhat, conforms accurately to the surface of the object, and adheres closely to it. In this way the holdfast of the new plant is begun. The cause of this local and peculiar growth cannot be due to the stimulation of gravitation, for such spores attach themselves as frequently to oblique and vertical as to horizontal surfaces. Nor can it be warmth or moisture, or even chemical stimulation. It must be either light or contact or both. Light or darkness must play a part in controlling the local growth of holdfasts in many plants. It appears, however, to influence locomotion and the direction of division of the spores* rather than to stimulate growth in the parts touching the solid object. We may conclude, then, that contact with the solid stimulates the protoplasm, but it remains for experiment actually to show that the increased rate and the changed direction of growth in such cases among plants are due to contact, though it seems to be the case in animals.*

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* Winkler. H. Einfluss äusserer Factoren auf die Theilung der Eier von Cystosira barbata. Ber. d. D. Bot. Ges., Bd. 18, 1900.

Among higher plants, familiar examples of growth stimulated by contact are afforded by those species of *Ampelopsis* which form the curiously branched organs of attachment shown in the accompanying figures (*A. Veitchii*). The young branches, "tendrils," (*a*) are soft, weak, tapering, long and slender, slightly enlarged at the tips and green only there. After the tips come into contact with a suitable vertical surface, they broaden and flatten out, pressing closely against the surface, forming the little discs which presently become very strongly attached (*b*). If the "tendrils" do not touch a surface suitable for attachment, the tips do not enlarge, the whole organ remains weak, and finally dies and falls away. Stability of the support and prolonged contact with it seem to be indispensable to the formation of the disc-shaped bodies. These are the larger the rougher the surface of the support, other things being equal. The subsequent thickening and strengthening of the "tendril" are due to mechanical pull (see pp. 187–8) rather than to the contact of the tips with a rough object.

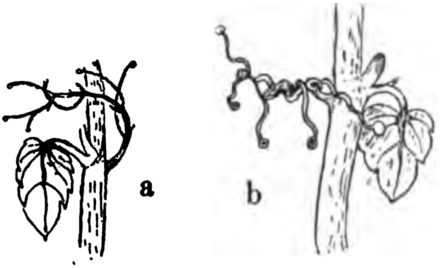

Figure 19.—Tendrils of *Ampelopsis Veitchii.* *a*, before, *b*, after attachment.

The direction of growth is controlled in many instances by contact with solid objects. *Thigmotropism* or *stereotropism* is the name proposed for this phenomenon. The most striking examples are furnished by tendrils,† which have been studied by many observers.

The sensitiveness of tendrils to contact varies greatly with the species, the prevailing conditions, and the age of the tendrils. They are most sensitive when they are half or three quarters grown and until after they have attained their full length. A considerable degree of warmth and humidity increases their sensitiveness, warmth being the more important factor. Most tendrils are more sensitive on one side than on the others. The part most sensitive to contact is that between the tip and middle, the tip itself and the base not being sensitive to contact. The base is, however, sensitive to gravity and in this respect differs from the rest of the tendril. The zones of greatest sensitiveness and of greatest growth, as in roots (see p. 201), are not coincident.

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* Loeb, J. Untersuchungen zur physiologischen Morphologie der Thiere. I. Über Heteromorphose. Würzburg, 1891.

† See Darwin's "Movements and Habits of Climbing Plants" and Pfeffer's Pflanzenphysiologie Bd. II., 2ter Theil. 2te Auflage.

A tendril of *Passiflora* in the right stage of growth and under favorable conditions will soon bend toward the side touched, if gently stroked with a pencil. The extent and duration of the bending will be proportioned to the degree of irritation. The rougher the surface of the object which the tendril touches, the more pronounced the bending. Because the surface of tendrils is so smooth, they so slightly irritate each other when they chance to touch that they rarely bend about each other. A succession of light touches, each too light to induce a pronounced or permanent bending, will stimulate a tendril to the same degree as continuous contact with the same object, but unless the contacts are made at very short intervals, so that the tendril finally catches and entwines the stimulating object, thereby producing an enduring contact and a prolonged stimulus, the tendril will cease to bend more and will finally straighten out. Presumably loss of sensitiveness precedes loss of ability to bend, but since the reaction is the only evidence we now have of the sensitiveness, it is impossible to say positively. This experiment shows, among other things, that there is an accumulation of stimuli, that the response is not immediate but induced, and that the tendril finally ceases to respond to one degree of inconstant stimulation, becoming either accustomed and unsensitive or else fatigued and unresponsive. This condition has its parallel in the familiar state of the fatigued muscle or organism. A fresh horse lightly touched by the whip responds to the slight stimulus by increasing his speed, but the same horse at the end of a hard day's journey cannot be made by the same stimulus, or even by a greater, to give the same response. This indicates two things: in the first place, that the touch of the whip or the repeated contact with a solid body do not of themselves increase the speed of the horse or accomplish the bending of the tendril, but that they are merely stimuli, that these slight influences set in operation other forces.

Our conception of the stimulus as merely the feeble force which sets other forces in operation is justified by further consideration of the behavior of horse and tendril. Though the fresh horse promptly responds to the light touch of the whip, there is actually the lapse of some time between stimulus and reaction, but this time is brief because the nerve and muscle systems of the horse are exquisitely adapted to receiving and responding to such stimuli. They are especially differentiated to accomplish a few purposes. The tendril responds more slowly to contact. There is what is termed the "latent period" between stimulation and reaction, ranging from five seconds or less to an hour or more according to the species, but during this period the forces set in operation by the stimulus are working.

The means by which a tendril curves around its support is not definitely known, and it may well be that the mechanics of curvature are not the same in all cases. The older plant physiologists, like Sachs* and de Vries,† asserted that the bending is due to changes in the rate of growth on the two sides, the side in contact with the support growing less rapidly, the opposite side more rapidly, than before the contact was made. MacDougal‡ dissents from this generally accepted opinion, believing that there are not such changes in growth-rate, but that the side in contact with the solid object contracts decidedly and that the opposite side may grow less rapidly than when the tendril is free. Presumably either the contraction of the cells on the side touched, or the expansion (fixed by growth) of the cells of the opposite side, would develop the mechanical force needed to accomplish the bending, for the resistance to be overcome is slight. Indeed, until they have attached themselves to a support and have developed strengthening tissues as a result of strain (see pp. 187–8), tendrils are mechanically weak as well as irritable.

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* **Sachs, J. von. Physiology of Plants. Eng. Edition, 1887.**

† **De Vries, H. Längenwachsthum der Ober- und Unterseite krümmender Ranken. Arb. d. Bot. Inst. Würzburg, Bd. I., 1873.**

‡ **MacDougal, D. T. Mechanism of curvature in tendrils. Annals of Botany, X., 1896.**

The irritability of tendrils varies greatly, the tendrils of grape-vine requiring prolonged contact with a comparatively rough object, those of passion-vine (*Passiflora*) responding to extremely slight and transient stimuli in 25 to 30 seconds. The size of the solid object must be proportioned to the size, structure, and sensitiveness of the tendril if it is to be successfully clasped. The tendrils of grape, for example, cannot twine about objects of small size, while tendrils of *Echinocystis* will coil about a spider's thread.* A piece of thread weighing 0.00025 milligram, placed as a rider on a tendril of passion-vine, causes no stimulus if motionless, but induces bending if swinging on the tendril.† All solids except moist gelatine irritate; no harmless liquid, free from solid particles, not even mercury, stimulates the most sensitive tendril to bend. From this we may infer that unless there be a certain amount of adhesion between the tendril and the object by which it is touched, there will be no irritation. This adhesion changes the pressure in the cells of the part touched, increasing or decreasing the pressure according to circumstances.

The petioles of several well-known plants are more or less sensitive to contact, *e. g. Lophospermum scandens, Solanum jasminoides, Tropæolum majus, Clematis.* The stems of dodder (*Cuscuta*) are also periodically sensitive to contact.‡ This parasite twines about its host, forming alternately the steep spirals typical of twining plants and short close spirals like tendrils. After it has sent haustoria into the tissues of its host, dodder elongates very rapidly for a few hours. During this time the stem is not sensitive to contact and it behaves like an ordinary twining plant, circumnutating and obeying the force of gravity. Presently, however, the rate of growth decreases and then it begins to be sensitive to contact. When irritated by contact with an object of suitable size, dodder will make two or three or even more close tendril-like turns about the support. It will not form these close coils about moist gelatine, it cannot twine about objects too large or too small. The longer the contact and the rougher the surface of the support, the more prompt and pronounced will be the bending. Only prolonged contact will induce permanent bending. This is the first effect induced by contact.

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* MacDougal, *loc. cit.*, p. 376.

† Pfeffer, W. Zur Kenntniss der Contaktreize. Untersuch. a. d. Bot. Inst. Tübingen, Bd. I, 1885.

‡ Peirce, G. J. Contribution to the physiology of the genus Cuscuta. Annals of Botany, VIII., 1894.

A second effect consists in the formation of haustoria, lateral root-like organs which the parasite sends into the tissues of its host and through which it draws needed food. Without contact these organs never form, even in rudimentary conditions. Without contact with an object able to furnish food as well as mechanical support to the parasite, the haustoria will not fully develop. Contact stimulus induces the stem to bend closely about the support and to form haustoria, but chemical stimulus is needed besides to secure the development of the haustoria. In fact, the seedling dodder will not even twine about innutritious supports. Furthermore, the dodder stem is sensitive to gravity and will not twine closely or otherwise about a suitable, even nutritious, support unless the position of this be vertical or only slightly inclined.

The dodders, and a few tropical plants like them (*e. g. Cassytha*), are exceptional twining plants. The great majority of twining plants are not sensitive to contact, and though they twine about vertical or nearly vertical supports of suitable size and form, they do so by the combined action of their spontaneous nutation movements and of gravitation. As Darwin so clearly demonstrated,* all growing parts, at least of vascular plants, are in constant motion, owing to their growth not being equal on all sides at any one time. The rate of growth changes in the different parts, and because this change in rate is fairly regular and takes place in adjacent parts successively around the plant or part, the motion is regular, circular or elliptical in a horizontal plane, spiral in space. Darwin called it circumnutation. Apparently the regularity of the motion is due to external stimuli rather than to causes inherent in the organism. Experiment* seems to show that the coöperation of the forces to which plants are constantly and successively subjected—*e. g.* gravitation, light, heat, etc.—reduces the otherwise wholly irregular movements to order and system, and that without these stimuli these movements produced by unequal growth are entirely irregular. The circumnutation of twining plants is through a somewhat wider orbit than that of other plants, probably because of their greater length in proportion to their thickness and mechanical strength. The tips of the stems and branches do not stand out straight for any great distance; they tend to droop somewhat. The negative geotropism and the ample nutation of the slender and elongated stems of twining plants cause them to grow spirally upward around suitable supports.†

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* Darwin, C. The power of movement in plants.

Sensitiveness to contact and later their parasitism were probably acquired by dodder and its allies after these plants had developed the twining habit. The nearest relatives of the dodder are still independent twiners, closely resembling the behavior of dodder in its unsensitive periods. Furthermore, under stress of insufficient food, the dodder is able to manufacture some food for itself. It will develop chlorophyll in the usually rudimentary and often otherwise colored chromatophores which it contains in large numbers.

Thigmotropic sensitiveness of other organs and of lower plants has been demonstrated by various authors,* though Sachs's claim that roots are sensitive to contact seems to have been successfully disproved by Newcombe.† Newcombe shows that roots do not bend about harmless substances (*e. g.* glass rods and splinters of tannin-free wood) although they do coil around pins, brass wire, and rods made of wood containing tannin or other injurious matters. The bendings which Sachs described were responses to injury (traumatropic) rather than to contact.‡ Studies of the thigmotaxis of plants are very few, if any at all exist, yet the behavior of such motile organisms as the diatoms, *Oscillatoria*, *Beggiatoa*, etc., and the relations of zoöspores to the solid substances to which they attach themselves, offer objects as interesting as they are difficult for investigation.

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* Fritzsche, Curt. Über die Beeinflussung der Circumnutation durch verschiedene Factoren. Inaug.-Diss. Leipzig, 1899.

† For a careful study of the mechanics of twining see Kolkwitz, R. Beiträge zur Mechanik des Windens. Ber. d. D. Bot. Ges., Bd. XIII., 1895. The literature is here cited.

Something must now be said about the so-called "sensitive plants." These respond to a touch, a blow, or even a sudden breath of air, to a drop or stream of water upon the leaves, as well as to changes in illumination, temperature, etc. These plants have compound leaves, the petioles of the leaves and the stalks of the leaflets being supplied with cushion-like enlargements called *pulvini*, which serve as an articulation between petiole and blade or between petiole and branch. A pulvinus is composed mainly of parenchyma tissue, the cell-walls of which are elastic and readily permeable to water. The fibro-vascular bundles which, in the petiole and in the blade of the leaf, are separated from one another by plates of parenchymatous tissue, are placed close together in the pulvinus forming an axial strand. This axial strand is the part of the pulvinus possessing greatest tensile strength, but the several layers of parenchyma cells by which it is surrounded are what expand or close, raise or lower, the leaflets and the whole leaf by changes in the amount of water which they contain, in other words, by changes in their turgescence. These parenchyma cells act as the cushion on which the blade of the leaf rests. As has been repeatedly described in the text-books, and in numberless works on "the wonders of Nature,"* the position of the leaves and leaflets varies, or may be made quickly to change, according to the conditions surrounding the plant. The accompanying figures illustrate the periodic changes occurring in the position of the leaves and leaflets of *Mimosa pudica* under normal conditions. Figure 20 *a* is the ordinary "day position," when the light is fairly strong, the air warm, and water sufficiently abundant to allow rapid transpiration without harm. Figure 20 *b* is the ordinary "night or sleep position," when the light is weak, the air cool and moist so that dew will form. Figure 20 *c* is the position taken when the illumination is so intense and transpiration so rapid that there is danger of excessive loss of water.†

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* Sachs, J. von. Über das Wachsthum der Haupt- und Nebenwurzeln. Arb. d. Bot. Inst. Würzburg, Bd. I, p. 437, 1873, and Ges. Abhandl., Bd. II, p. 826, 1893. Errera, L. Die grosse Wachsthumsperiode bei den Fruchtträgern von Phycomyces. Bot. Zeitung, Bd. 42, 1884. Wortmann, J. Zur Kenntniss der Reizbewegungen. Bot. Zeitung, Bd. 45, 1887.

† Newcombe, F. C. Sachs' angebliche thigmotropische Kurven an Wurzeln waren traumatisch. Beihefte z. Bot. Centralbl, xii., 1902.

‡ Spaulding, V. M. The traumatropic curvature of roots. Ann. of Bot., viii., 1894.

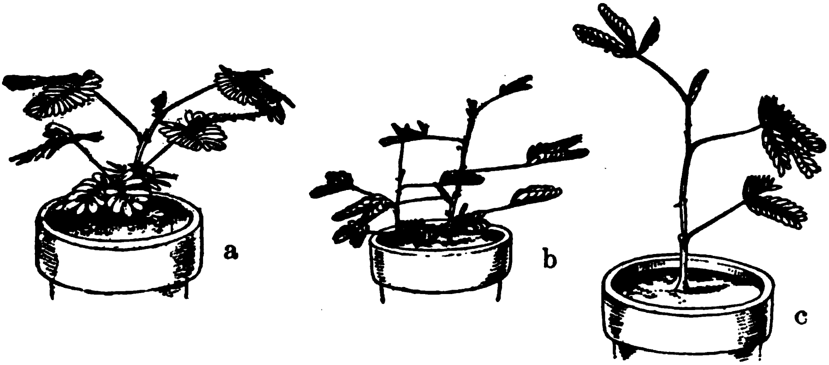

Figure 20. "Sensitive Plant" (*Mimosa pudica*) by day (*a*), by night (*b*), and in light and air of excessive brightness and dryness (*c*). From MacDougal.

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* For example, see "Living Plants and their Properties," by Arthur and MacDougal, Chapter IV., New York, 1898, from which the following description is mainly drawn.

† For a discussion of these movements with relation to transpiration see pp. 141-2.

The plants of *Mimosa pudica* shown in the accompanying figures (21) were stimulated not by touch but by a small flame, though a touch or blow of sufficient force would produce the same effect. The figures therefore illustrate what there is to say of the relations of this plant to contact. Comparing these with figure 20 *a* on p. 248 we find that under favorable conditions of light, temperature, moisture, etc., lightly touching one or more of the leaflets of a plant with the finger, a pencil or some similar harmless instrument, will induce the leaflets to move quickly upward toward one another and slightly forward, so that they come to lie closely face to face along the leaf-stalk. An exceedingly light touch may induce only one leaflet to move, a touch less light will induce both leaflets of a pair to move, one still stronger will stimulate adjacent pairs and finally all the leaflets of the compound leaf to close. At last the main petiole of the whole leaf sinks, bending at its pulvinus, as is shown in figure 21 *b*. If the touch be sufficiently strong, a blow rather than a touch, the other leaves and leaflets will behave in all respects similarly (figure *c*) until finally the appearance of the plant will be such as indicated by figure *d*.

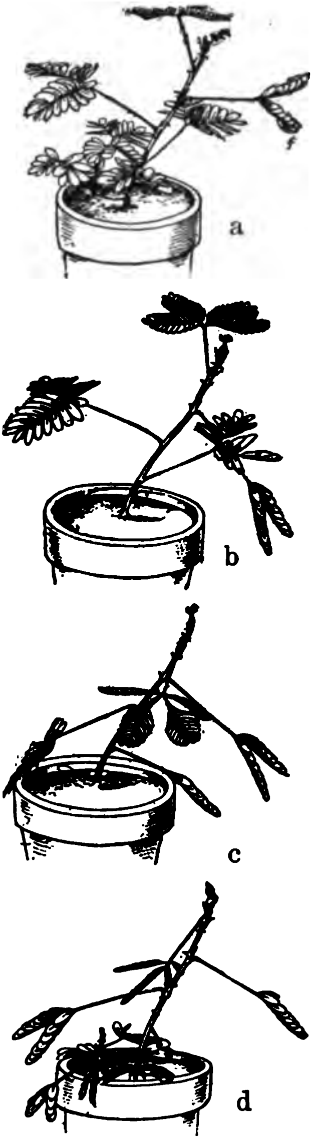

Figure 21. Sensitive Plant in various stages of stimulation. From MacDougal.

Although evidently there is still much work to be done before the subject will be quite clear, it appears from already published investigations that the means by which the leaves and leaflets are moved are found in the parenchyma cells of the pulvini.* These cells, taking up water from the adjacent vascular elements in the axial strand of bundles, expand, become turgid, and exercise sufficient force to raise the petiole or the blade respectively of the leaf or leaflet above. The opposite effect follows, leaflet, leaf, and petiole droop when, for any reason, the parenchyma cells of the pulvini, giving up the water which they contain to the vascular elements, become smaller, flabby, and contracted, if not collapsed.

A great variety of stimuli set in motion the mechanism by which the leaflets and leaves are closed. What is the use of these movements, and what is the means of transmitting the impulse to move, are by no means clear. Stahl,† from observations made in the tropics, confirms Darwin's claim that the closing of the leaves is an effective protection, in connection with the thorns which the plant bears, against hungry herbivorous mammals. It is seemingly probable that contact and various other stimuli cause the contraction of some of the cells in the leaf and that, in their contraction, these cells expel water into the vascular elements or intercellular spaces. The contraction of any cell or group of cells will necessarily affect the tensions of adjacent cells. Thus, though we cannot conceive of the transmission of the impulse itself from cell to cell, yet we can readily conceive of the extension to an increasing number of cells of the conditions first produced by the irritant acting upon a small number of cells. *Mimosa* is not able to respond to stimulus (whether it is then sensitive or not is another question) when under the influence of an anæsthetic or in a state of chill, heat-rigor, etc. For this reason the inference is easy that the physical changes induced by stimuli are transmitted only through living cells. This is not necessarily the case, as MacDougal's experiments tend to prove.* Haberlandt† claims the transmission of the stimulus through tubular series of cells in the phloëm of the vascular bundles. Since Fischer‡ has shown the continuity of the sieve-tubes throughout the plant, it is not unlikely that Haberlandt's tubes are also continuous and may therefore furnish at least one course along which the changed turgor of any group of cells could affect other cells.

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* Stahl, E. Über den Pflanzenschlaf und verwandte Erscheinungen. Bot. Zeitung, 1897. Cunningham, D. D. The causes of the fluctuations in the motor organs of leaves. Annals of the Botanic Garden, Calcutta, vol. VI., 1895. MacDougal, D. T. The mechanism of movement and transmission of impulses in Mimosa and other "Sensitive" Plants: a review with some additional experiments. Bot. Gazette, XXII., 1896. Haberlandt, G. Das reizleitende Gewebe der Sinnpflanze, Leipzig, 1890. Sinnesorgane im Pflanzenreich. Leipzig, 1901.

† Stahl, E. *l. c.*

The stamens of barberry and of some of the *Compositæ*, and the stigmas of *Mimulus*, *Torenia*, etc., contract on being touched. Presumably these, and other similar movements, are due to decreased turgor in the parenchyma cells forming a considerable part of the organ, as well as in *Mimosa*.

CONCLUSION

So far we have separately considered the operations of the more evident influences which direct plants in growth and in other activities. This process of analysis leads us to more definite views regarding the effects of these different forces acting as stimuli, but in nature the plant is subjected to all of these forces more or less constantly and more or less simultaneously. Thus light and gravitation may be acting simultaneously and, because of the action of both, the response of an organ to either force will not be the same as if that one were acting alone (see p. 214). Moisture, warmth, contact, and chemical substances may also be acting upon the plant at the same time. The behavior of a plant, then, expresses its adjustment to all the influences operating upon it. Its size, form, color, vigor, etc., represent its response to all the stimuli it has received.

Furthermore, as conclusively proved by recent experiment,§ whatever stimulates or otherwise affects one part or organ affects all the other parts of the plant. Injury or loss of a part is always followed in healthy plants by the replacement of the part, either by new tissues, or by another part assuming the work of that injured or lost. Thus, if the tip of a pine or other perennial with excurrent stem is injured, the lateral branches change their direction of growth, and finally the strongest and most rapidly growing of these assumes the direction and functions of the main stem. "Cutting back" stem or root is followed by copious branching. When, as in floating specimens of *Marsilia*, etc., enough water is absorbed by other parts, the roots soon cease to grow and may even finally disappear.

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* MacDougal, D. T. *l. c.*

† Haberlandt, G. *l. c.*

‡ Fischer, A. Neue Beiträge zur Kenntniss der Siebröhren. Ber. d. math.-phys. Classe d. K. Sächs. Ges. d. Wiss., 1886.

§ Hering, F. Über Wachsthumscorrelationen in Folge mechanischer Hemmung des Wachsens. Jahrb. f. wiss. Bot., Bd. 29, 1896. Kny, L. Correlation in growth of roots and shoots. II. Ann. of Bot., XV., 1901. Other papers cited by these authors, and by Pfeffer, Pflanzenphysiologie Bd. II., Theil 1 1901.

We must conclude, then, that the plant is sensitive as a whole because of the sensitiveness of its parts, that the condition of one part affects all the other parts, that correlation is a necessity if the organism is to act as an individual or even as an association of coöperating members.

Besides the forces which, through analysis, we have been able to recognize distinctly, there are complex influences consisting of forces and influences which have so far eluded analysis. The analytical method has not yet exhausted the subject; more detailed physical and chemical knowledge will come presently. Meantime it is more or less the fashion, under the name of ecology, to view things in the large way, and by feeling rather than by the application of exact physiological methods, to reach conclusions regarding the effects of environment and of association. The trees of a given species, presenting one appearance when they grow as members of a thick forest, are very different when growing separately in the open. These differences in appearance are due in great part doubtless to differences in the amounts of light and food, of mechanical strain, and of room, but these are not all, nor do we know the relative importance of the separate influences. We do not know why small plants of characteristic species are the regular associates of certain kinds of trees.* Such phenomena show that plants are sensitive to all the forces and influences which we combine without analysis under the name environment, and that the coöperation of these influences induces, *as reactions* in the living plants, the qualities which we see and call characteristic of the species, order, or class—reactions which are really characteristic only of the living protoplasm. Protoplasm is not all equally sensitive to any one influence or to the whole complex of influences which constitute its living and lifeless environment. These different degrees of sensitiveness, coupled with different powers of response, are what bring about, in the same environment, the forms, sizes, colors, etc., which characterize individuals and species.

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* For example, see Höck. F. Begleitpflanzen der Kiefer in Norddeutschland. Ber. d. Deutsch. Bot. Ges., Bd. XI., 1893; Coulter, Plant Relations, New York. 1899, etc.

The various forces operating upon the living organism set up and maintain in it physical and chemical conditions which can be changed only by the introduction of a new force or by a change in the relative proportions of the old forces. The living differs from the dead organism and from all lifeless compounds and structures in the supreme delicacy of its structure, due to the arrangement, complexity, and instability of the compounds composing and contained within it (see pp. 183-6). The sensitiveness of living organisms is different in degree and not in kind from that of lifeless things; the sensitiveness of both is a matter of physics and chemistry.

CHAPTER VII

REPRODUCTION

The subject of reproduction has been more fully and more exactly studied by morphologists than by physiologists. It has been meditated upon more than it has been investigated through experiment. Yet there are certain results of comparatively recent work, and there are certain hypotheses, which must be considered in any discussion of the physiology of plants.

In the vegetable as in the animal kingdom the span of life of the individual organism is limited. In many cases it is limited by perfectly obvious influences; in most it is limited by means little understood even if apprehended at all. In many plants and animals there are no evident reasons inherent in the organisms themselves why they should not continue to live indefinitely. Influences wholly external and only slightly controllable by the organism determine and terminate its career. The effects of these influences are to be distinguished from the irritable responses which we have studied in the preceding chapter. Irritable response depends upon a degree of sensitiveness possessed only by the living organism, although this sensitiveness is dependent upon the sum of the physical and chemical conditions prevailing in the organism (p. 186). But the influences which terminate its career exceed the powers of resistance, reaction, or response, of the organism. They act upon it as upon any lifeless thing of similar composition and structure, and they produce on the lifeless similar effects to those produced on the living body. For example, the heavy wind which uproots a tree would bring it to the ground were it alive or dead. Uprooted it would dry faster than if its roots were still in the soil. It is after all the drying, following the uprooting, and not the uprooting itself, which is the fatal thing. Again—the frost which kills a living herb would produce in another similar but lifeless herb the same injurious mechanical changes, which neither living nor lifeless herb could obliterate or reverse and recover from. Excessive shade or light injure and may be fatal to living plants, the former entailing insufficient food-manufacture, the latter causing undue activity in this or in other ways. Lifeless structures as sensitive to light will also be affected by the same means; the photographic plate is injured or ruined by insufficient or by excessive light.

From these examples the inference is obvious that, if the conditions which make life possible (p. 6) were maintained, many organisms which now die at the end of a season or a cycle, would continue to live. The inference could not, however, be extended to all plants, because what determines the span of life of the organism is often within it, not outside. This every one knows. Wheat harvest comes long before frost or heat or drought can terminate the lives of the wheat plants. In California the wheat plants are dead before harvest begins. They have ceased to live when they have matured their fruits. They have transferred to the embryos in the fruits the life which they themselves possessed. The one living wheat stalk has formed several or many kernels, each containing a living plantlet. Among these new individuals the life of the parent has been completely distributed. The parent stalk ceases to live, its life is ended, the parent lives only in its offspring. No external influences have contributed to the death of the stalk except as they have contributed to its successful life and to its production of successors. So it is with other plants which fruit once and then die, whether fruiting take place in a month, a season, or a "century." By preventing fruiting, man can artificially prolong the life of many such plants. The flowering plants of our gardens are induced to continue blooming and to live longer by being kept from setting seed. By constantly picking the flowers of sweet-pea, pansy, etc., larger, handsomer and more numerous flowers may be had for a longer time than if the life of the individual plant were allowed to pass over into the new individuals represented by the embryos in the seeds. The life cannot pass over, however, without a physical basis; the substance of the parent is given to and forms the offspring. The giving of substance and of life are simultaneous if not identical. When this gift exceeds a certain amount, the parent ceases to be, it abandons its own body, it lives only in its offspring. Internal causes are what terminate the lives of plants like these, but as we shall presently see (pp. 263-76), these are profoundly affected by external influences.

There are other internal causes which may terminate the life of an individual. If its parent endow it so badly with substance, form, or food that it cannot maintain the balance of constructive and destructive processes in which living consists, it will die. Its span of life is determined by its own substance, structure, and energy, all of which, or the means of gaining which, were given it by its parents. Such an individual, unable to live long enough to produce offspring, ceases to live because its internal balance breaks. Its life ceases because destructive processes exceed the constructive. Its lifeless substance thereupon becomes the source of matter and of energy for living individuals of other kinds.

Since living may be said to consist in maintaining the balance between construction and destruction, life may be said to represent the balance of energy-storing and energy-liberating processes. There is as much substance and as much energy when there is no balance. When the balance is attained, there is life; when the balance is not attained, there is no life. When an individual dies without offspring, there is less life in the world but no less substance or energy. When an individual, having given sufficient substance in suitable form to its offspring to start them in their careers, continues to live for a time, there is less life when it dies but no less matter or energy. There is simply a different adjustment of forces, a different arrangement of matter. But this different adjustment is merely local, more or less individual. The population of a given locality may greatly increase, but with the increase in number of human beings there is a decrease in the number of living organisms of certain other sorts. The multiplication of the individuals of one species may often result in an increase in the number of living organisms in the locality, but there is no evidence that, as a whole, the living population of the earth is increased. Reproduction is not a process by which more is made out of a given amount, for, if this were so, the beginning would be the making of something from nothing. Force and matter remaining constant, reproduction can only maintain, it cannot, beyond a certain point, increase the total number of living organisms.

We are thus led to see that reproduction is a process of which the chief end is maintenance and increase of the species rather than the increase in life. The command "Be fruitful and multiply" is coupled with the law which irresistibly forbids increase beyond a certain point. As characteristic of the living substance as breathing or feeding is the tendency to maintain and to perpetuate itself. Only by securing more supplies of matter for replacing worn-out parts, and of energy for carrying on its functions, does the living organism maintain itself. When it secures more matter than is needed to repair, and more energy than is needed to operate, already existing parts, it grows. When for any reason growth beyond a certain characteristic size is impossible or difficult, while the supply of matter and energy continues the same, there must be some other mode of increase of the individual, whether cell or organism. The one individual, cell or organism, after forming new substance (protoplasm) and furnishing it with energy (heat, etc.), may finally separate this as a new individual. The mother cell divides it off as a new cell, the parent organism separates it as a reproductive body, a sperm or egg, a spore or seed, an embryo or a larva. Reproduction has been defined as "Growth beyond the limits of the individual." Like growth, it depends upon the successful performance of the ordinary functions, and it simply insures their continuance.

Again, reproduction is said to be "the effort to bridge the gap of death." This definition is suggestive but misleading. By reproduction living is continued; the life, the substance, and the activities, of the offspring were those of the parents. There is no gap or break, there is perfect continuity. If a gap were to occur, nothing could bridge it, there would be nothing with which to bridge it, the species or the race would be extinct. A new creation would be necessary, and experience does not encourage belief in new creations. Reproduction, then, prevents the formation of a gap. When death comes to an organism which has already formed a new individual consisting of and continuing the substance, structure, and activities of the old, death effects no break, there is no gap. When death comes to an organism which has not yet grown beyond itself, a gap is formed, but formed too soon ever to be bridged or closed.

The chief end of reproduction is, then, the maintenance of life, the continuity of the species. Another end is only less important, that of increasing the number of individuals. The parent stalk of wheat which has given all its living substance to the two dozen or so new individuals enclosed within the kernels it has produced, is contributing to increase the number of wheat individuals living next year. As we know, there will be no real increase, however, unless these kernels fall into spots where no plant or only a weaker one lived before. Under natural conditions, which have so long remained the same that the possibilities of the situation are as fully exploited by the organisms living there now as can be the case at the present stage in evolution, there will be no vacant spots in which an increased number of individuals can live. Under these conditions reproduction cannot effect an increase, it can only continue the life, of the species. However, when any new factor is introduced, when seismic disturbance, or climatic change, or the entrance of some new and powerful organism, modifies the conditions, each new individual in a brood or crop has a different chance from before, a better chance or a worse according to the relative characters of the new individual and of the changed environment. Those organisms which have young ready and able to take advantage of the changed environment will thereby have a better chance to increase their kind as well as to maintain it. As the maintenance of the species is always more important than its increase, and as the increase of the species is only sometimes possible, such a system of reproduction as will best serve the chief end has been developed by every successful organism. Many organisms possess one means of reproduction which combines these two ends, others have different means leading to the two ends separately.*

Two modes of reproduction, almost universal in their occurrence among plants, can be distinguished, the sexual and the non-sexual. In the former, two cells from two different sources unite and thereby form a new individual. In the latter, the new individual is developed from one cell or from a group of cells. The difference between these two would seem very clear were it not for the fact that it sometimes happens spontaneously in nature, and may be made to happen in a considerable number of cases in the laboratory, that one of the sexual elements (cells) develops into a new individual without first fusing with the other sexual element (cell). The development of one sexual cell into a new individual without first fusing with the other sexual cell is called parthenogenesis. Parthenogenesis is, in effect, the same as non-sexual reproduction. Morphologically, sexual reproduction differs from non-sexual reproduction in the fusion of two cells into one. Physiologically, sexual reproduction differs from non-sexual reproduction in the causes which lead to it and in the results produced by it. In sexual reproduction, one cell is "fertilized" by the fusion with it of the other sexual element. In non-sexual reproduction the cells are "fertile" without this fusion. "Fertilization" has been regarded as giving the stimulus needed by the sexual cell for development as a new individual. Non-sexual reproductive cells do not require this stimulus to develop as new individuals. In natural parthenogenesis, the one sexual cell, the egg-cell, also develops as a new individual without the stimulus of fertilization. In parthenogenesis artificially produced in the laboratory, chemical or other stimuli applied to the eggs cause them to develop as new individuals.* So far, individuals thus produced have not developed to maturity, though this may be expected to be attained. There is, however, an essential difference between individuals produced on the one hand by non-sexual means, by natural parthenogenesis, and from sexual cells artificially stimulated, and on the other hand by sexual means—the fusion of two cells. In the latter case, the one cell absorbs not only simple inorganic compounds, but also all the complex organic compounds contained in the other sexual element; the *structure* as well as the *substance* of the two cells unites; two sets of *organs* are combined into one; nucleus fuses with nucleus, cytoplasm with cytoplasm; the *individual characters of the two cells are combined in the new individual.* We see, then, that fertilization is more than stimulation; it is union.† In this union of structure, organs, and characters, although these are composed of chemical compounds, the definite arrangement of the parts in the sexual elements is as essential as the composition of the parts. The result in the new individual will vary with the arrangement of the parts in each sexual element. In other words, there is not only a chemical basis to fertilization; there is also a mechanical. Fertilization cannot be complete and perfect without both chemical and mechanical effects. What the significance, and what the relative importance, of the chemical and mechanical factors in fertilization may be is now the subject of hypothesis and experiment. The matter is far from settlement.

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* What these means are, may be learned from Campbell's University Text Book of Botany, New York, 1902.

That there are advantages in a mode of reproduction which unites chemical and mechanical effects, and in development which follows only after these are produced, would seem to be indicated by the development of sexual reproduction by so many different types of organisms. If non-sexual reproduction were the more successful mode of reproduction, would its relative importance be so greatly reduced among higher organisms, both plants and animals? Yet what the advantages of sexual over non-sexual reproduction are, is by no means certain.

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* Loeb, J. Artificial production of normal larvæ from the unfertilized eggs of the Sea Urchin (Arbacia). Amer. Journ. Physiology, vol. III., 1900. Experiments on artificial parthenogenesis in Annelids (Chaetopterus). *Ibid.* vol. IV., 1901. Nature of the process of fertilization. *Ibid.* vol. IV., 1901. Matthews, A. P. Artificial parthenogenesis produced by mechanical agitation. Amer. Journ. Physiol., vol. VI., 1901.

† Strasburger, E. Über Befruchtung. Bot. Zeitung, 1901. Boveri, Th. Das Problem der Befruchtung. Jena, 1902.

Between animals and plants there are striking resemblances in the processes which constitute and succeed sexual reproduction. Fertilization and the formation of new individuals are the same in the two kingdoms, and the care of the young between the times of their conception in the body of the mother and of their separation from it also correspond. Only among the highest animals, the *Mammalia*, is the care of the offspring carried beyond what is found among plants. The plant-mother cannot nourish her offspring after it has been separated from her body, though she has supplied it with a store of food. The mammalian mother can and does. This difference of degree in development does not, however, make our comparison less suggestive.

One point more needs emphasis in this connection. Since the continuity of the species is the chief end of reproduction, precautions to ensure its attainment must be taken. The lower plants like the lower animals, simple in structure and small in size, as a rule rely on the survival of some of their numerous and but slightly developed offspring rather than upon the better equipment of a smaller number of more completely developed young. Among higher organisms, the opposite is the general rule. The relatively small number of the seeds of the *Leguminosæ*, each seed containing a large, well fed, and highly developed embryo, may be regarded as typical of the higher plants, while the small, not fully developed embryos of the *Orchidaceæ*, *Ericaceæ*, etc., in the seeds of which only small quantities of food are stored, represent a distinctly lower type.

There are two kinds of non-sexual reproduction, the vegetative and the spore. In the former a mass of tissue, capable of carrying on many functions and of developing into a new plant, is separated from the single parent. In the latter, a single cell or, at most, two cells together are cut off. These, though formed sometimes by the coöperation of many cells, are never formed by the fusion of cells. Each of the cells cut off is able, by successive divisions, to form a new plant like its parent. The one parent or parent-cell or mass of cells gives its own matter and energy, its own protoplasm, to the new individual. Because the substance of only one parent goes into the offspring there is a radical difference between this non-sexual mode of reproduction and the sexual mode. With the transfer from parent to offspring of its own substance and means of obtaining energy there are transferred also the same degree of sensitiveness, the same powers of reaction to stimuli, and the results of the reaction to stimuli already accomplished by the living protoplasm of the parent. The offspring are not only *like* the parent, they are really branches or continuations of the parent. There is introduced into the new individual nothing new, but as soon as it is cut off from the parent, it is subjected to influences some of which may be new and different and which will stimulate the individual to corresponding reactions. The gemmules of certain *Marchantiaceæ*, the lateral branches which gradually become the separate plants of *Azolla*, the runners of the strawberry, etc., are means of non-sexual (and vegetative) reproduction. The matter and energy, the substance and structure, of the one parent are carried directly over into these offspring. The condition of the parent at the time of reproduction, representing the resultant of all its reactions to all the stimuli to which it has been subjected, is also the condition of offspring made in this way. This fact is still clearer in such a plant as *Spirogyra*, which, breaking up into the cells of which the filament is composed,* forms new individuals which share its qualities by sharing its substance and structure. In many other low plants the process of vegetative reproduction is as simple and clear as possible. Similar but multicellular bodies vegetatively reproduce higher plants, continuing and at times multiplying the species with nearly or quite the same characters in the new as in the old individuals. The runners of strawberry, the suckers of lilac and *Sequoia*,* the stolons, offsets, runners, etc., of other plants, illustrate this matter.

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* **Benecke, W. Mechanismus und Biologie des Zerfalles der Conjugatenfäden in die einzelnen Zellen. Jahrb. f. w. Bot., 32, 1898.**

In the spore mode of non-sexual reproduction single cells or pairs of cells, each capable of forming a new plant, are cut off by the parent. These reproductive bodies, like the vegetatively reproductive bodies above mentioned, contain and continue the substance and the condition of the one parent. So soon as they are separated from the parent, they may be so influenced by the factors of their environment as to depart from the character of their parent, to vary.

The new individuals produced by non-sexual means are usually more numerous than those produced sexually. Non-sexual reproduction is especially the means by which the species is multiplied. Many species, however, have only one means of reproduction, hence the two ends, of maintaining and of multiplying the species, are met by the same means. Many organisms, however, endowed with both means of reproduction, employ one at one time, another at another time. What determines the organism in its behavior? And what are the advantages of each mode? The first question is answerable at the present time through the already available means of experimenting; the second is not definitely answerable now, though the interpretation of what is observed in nature, and speculation partially supported by experiment, suggest probable answers. From *Œdogonium* and *Coleochæte* among the green algæ to the highest of the flowering plants, the phenomenon of alternating generations is one of the most conspicuous in the life of plants. How this has originated and the influences which now control it constitute one of the most intricate problems in morphology and physiology, the solution of which remains, however, hidden in the future.

The preceding chapter has shown us that the size, form, color, rate of growth, direction of growth and of movement, and many other characters, represent the reaction of the organism to the external influences, its response to the stimuli, which are collectively termed its environment. We are, therefore, inclined to believe that its reproduction and its reproductive processes may also be similarly affected. Yet this belief is so modern as to be almost heretical. The morphology of reproduction has been studied by many; very few have engaged in experimental studies of the physiology of reproduction among plants. Of these few Sachs, Vöchting, and Klebs merit first mention. These men have shown that upon external influences quite as much as upon so-called inherited impulses depend the various kinds and stages of reproduction.

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* Peirce, G. J. Studies on the coast redwood. Proc. Cal. Acad. Sciences. 3d series, Botany, vol. II., 1901.

Klebs* studied certain algæ and fungi in order to determine the conditions under which they reproduce themselves. By experiment in culture he found that when certain conditions prevail, *Vaucheria* will form zoöspores, under other influences it will develop sexual organs and reproduce itself through them. These conditions are represented in tabular form thus:

VAUCHERIA SESSILIS †

ZOÖSPORES	SEXUAL ORGANS
Darkness after sufficient illumination for adequate food-manufacture invariably induces zoöspore formation. This will continue in darkness till there is no longer enough food, though there may still be enough for slow growth.	Light absolutely necessary for the formation of sex-organs. Light sufficient for healthy growth may be insufficient for formation of sex-organs. Strong light needed. Light, apart from its effect on nutrition, is a direct stimulus to form sex-organs.
The addition of water to a culture in damp air induces active zoöspore formation.	Sex-organs form either in damp air or in water; better in the former.
Temperature of 3° C. inhibits zoöspore formation in all but acclimated forms.	Same for sex-organs.

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* Klebs, G. Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. Jena, 1896. The literature is here cited. A second volume, treating of the general questions of the physiology of reproduction in low organisms, is promised, but not yet published (1902). *See also* Jahrb. f. wiss. Bot., Bd. 32, 33, 35. Falck, R. Die Bedingungen und die Bedeutung der Zygotenbildung bei Sporodinia grandis. Beiträge z. Biol. d. Pflanzen, Bd. VIII, 1901.

† Klebs divides this species into three. The names of these, and the reasons for division, not being essential in this connection, I retain the old name.

ZOÖSPORES	SEXUAL ORGANS
3°-8° are constant stimulus to zoöspore formation.	Sex-organs form, but develop more slowly than at higher temperatures.
26° is maximum temperature for zoöspore formation but not for growth. No acclimation to this.	Same for sex-organs.
10°-20° are indifferent temperatures, exercising neither stimulating nor depressing effects in passing up or down.	Same for sex-organs.
Raising temperature from indifferent to high, or lowering from indifferent to low, exercises no stimulus; *but* raising from 3° to 15° stimulates.	Same for sex-organs.
Culture in inorganic nutrient solution favors nutrition and growth, but not zoöspore formation. Transfer from such to less nutritious acts as stimulus to zoöspore formation.	Same for sex-organs.
Sugars and other nutritious organic compounds do not stimulate to formation of zoöspores.	Favor formation and development of sex-organs.
More oxygen required than for growth.	More oxygen required than for zoöspore formation.
Flowing water, by favoring nutrition and growth, retards or prevents zoöspore formation. Conversely, transfer to still water acts as a stimulus. Accommodation to still water followed by rapid growth and cessation of zoöspore formation.	No fertile plants in running water. Become fertile in still water.

From this table certain influences stand out as especially efficient stimuli to the formation of reproductive bodies. Thus *light*, which furnishes the energy for the manufacture of the materials needed to form the sexual organs and elements, must fall upon the plant in intensity, not only sufficient for this, but also great enough to act as a distinct stimulus to use the manufactured substance in this special way. Light furnishes the energy for one kind of work; more energy of this same kind sets and keeps other processes in operation. *Food*, when available in abundance, thus relieving the plant of the necessity of diligently manufacturing food for itself, stimulates to sexual activity, as is shown by the formation and activity of the sex-organs. This seems to be universally true in nature. Given the need of food and the means of manufacturing or obtaining it, the plant will be so especially engaged in the processes of nutrition that reproduction is not undertaken. But on the other hand, given a sufficient supply of food stored in its own body and diminished or suspended means of manufacturing more food, the plant will produce for a time in still water both zoöspores and sexual elements, while in the dark the formation of zoöspores (not of sex-organs) will continue for some length of time.

If plants are healthy, certain conditions will invariably induce them, whether they are old or young, to remain sterile. Certain other conditions will induce them to form bodies for their non-sexual reproduction, still other conditions will induce them to reproduce sexually. Reproduction then must be regarded, like movement, as a reaction or response to stimuli. But just as stimuli the same in kind and degree induce one response or the opposite or none at all, according to the kind of organism, so in reproduction, a stimulus or a combination of stimuli which induces one kind of plant to reproduce itself sexually may induce other kinds to reproduce themselves non-sexually or not at all. This may be illustrated by Klebs's studies of *Hydrodictyon*. This plant, the water-net, lives in still or only slowly running water, under normal conditions floats, and is physiologically as well as mechanically a very sensitive organism. It possesses two very distinct methods of reproduction, by non-sexual zoöspores, and by sexual motile spores or gametes. Gametes and zoöspores are formed in the ordinary vegetative cells, not in specially differentiated organs. Until these cells have attained a certain, though very minute, size they cannot form reproductive bodies. Whether there is a maximum size or not cannot be positively stated. Since gametes and zoöspores form in vegetative cells indistinguishable from each other, and since all or some of the cells of a net will form zoöspores or gametes or neither, it is obvious that each cell possesses in equal measure the ability to reproduce itself by zoöspores or by gametes. Observation shows that the same cell never reproduces itself by both means. External influences must, therefore, swing the balance in one direction or the other.

The following is a table showing the results of Klebs's experiments on Hydrodictyon:

HYDRODICTYON UTRICULATUM

ZOÖSPORES	GAMETES
Light absolutely necessary to zoöspore formation, strong light most favorable.	**Light not absolutely necessary.**
Darkness checks zoöspore formation.	**Darkness favors gamete over zoöspore formation.**
Transfer from darkness to light stimulates.	**Transfer from light to darkness stimulates.**
Flowing water retards or prevents zoöspore formation, still water stimulates, considerable volume needed.	**Small volume of still water stimulates gametes to form.**
Inorganic nutrient salts very strongly induce zoöspores to form. Zoöspores especially abundant when transfer in the light from nutrient solution to water.	**Inorganic nutrient salts retard gamete formation.**
Cane sugar not stimulating.	**Cane sugar in 0.5%-10% stimulates.**
Maltose very stimulating in light.	**Maltose and cane sugar stimulate in darkness.** **Cells with slight tendency to zoöspore formation produce zoöspores in lighted, gametes in darkened maltose solution.**
32° maximum temperature for zoöspores.	**33°-34° maximum temperature for gametes.**
8° too low temperature for zoöspores.	**Same for gametes.** **Slightly higher temperature will retard zoöspore and stimulate gamete formation.**
Only floating nets form zoöspores.	**Nets grown on filter paper wet with water, or better, with cane sugar solution, form gametes.**

This table shows that those conditions which contribute to increase and to maintain those activities which supply the plant with food, also favor reproduction by non-sexual means. Light, enabling the plant to manufacture carbohydrates, and the salts needed in elaborating carbohydrates into amides and proteids, stimulate zoöspore formation. On the other hand, the copious supply of already elaborated carbohydrates, especially when no unusual amount of inorganic salts stimulates to the further elaboration of carbohydrates into amides and proteids, is most favorable to the formation of gametes. Light is a specific stimulus to zoöspore formation, apart from its influence on nutrition. Given a vegetating cell, healthy and of such size that it can divide into zoöspores or gametes, it will continue to vegetate until it is subjected to some influence which will cause it to grow more slowly or to cease growing, and which will stimulate it to reproduce itself in the one or the other of the two ways in which it can reproduce. *Hydrodictyon* shows plainly that the time and the manner of reproduction are not fixed, but that both are determined by the influences to which the plant is subjected and is sensitive. Additional evidence of this is furnished by Klebs's observation that *Hydrodictyon* nets with an already marked tendency to form zoöspores can be so influenced by external conditions that they will cease to form zoöspores and will thereupon produce gametes instead. The same net, darkened at one end and illuminated at the other, will form gametes in the one end, zoöspores in the other, respectively.

Livingston* has studied one of the polymorphic algæ, a *Stigeoclonium*, particularly with a view to determining the influence of varying concentrations of the medium upon the form and reproduction of the plants. He finds that decreased osmotic pressure acts as a stimulus to zoöspore-formation as well as favoring vegetative activities, and that high osmotic pressure checks zoöspore-formation and the vegetative activities. This corresponds with Klebs's observations, but puts one part of them in somewhat more definite terms.

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* **Livingston, B. E. Nature of the stimulus which causes change of form in polymorphic algæ. Bot. Gazette, vol. 30, 1900. Further notes on the physiology of polymorphism in green algæ. Bot. Gazette, vol. 32, 1901.**

We see, then, that so far as the fresh-water algæ and certain fungi are concerned, plants react in reproduction, as in other ways, to external influences. In regions where there are clearly marked seasons, during one of which active vegetation is impossible by reason of extreme cold or darkness or dryness, these violent conditions determine the behavior of the organisms living there. In milder seasons and in more constantly temperate regions, more moderate influences determine their behavior. Of the forces which act upon algæ, stimulating processes which can be accomplished without them, light and heat are evidently the most important. A certain minimum amount of heat is a necessary condition of life; without it action is impossible; but given this minimum amount, more heat will stimulate to reproduction. A certain minimum amount of light is the necessary source of the energy for food-manufacture, but given this amount, more light will stimulate to some form of reproduction. Neither this larger amount of external heat nor the more intense light is necessary as a means of carrying on reproduction; they only set in operation that succession of processes which terminates in the formation of new individuals. Among the fungi, Klebs* claims that changes in the nutrition furnish the stimulus to a well-nourished mycelium to develop reproductive organs.

Vöchting's work on the conditions of reproduction in flowering plants† yielded results with which those of Klebs harmonize. Flowers are the visible agents of sexual reproduction in higher plants. When they are suppressed, or even are imperfect, sexual reproduction does not take place. Sexual reproduction in higher plants consists, as in lower forms, in the union of the microscopically small sexual elements. The forces which institute, stimulate, and favor sexual reproduction can, therefore, be ascertained by studying those forces which influence the conspicuous parts, the flowers. A force which must attain a certain strength before it will stimulate the plant to blossom, and without which the plant blossoms but imperfectly if at all, is one which controls sexual reproduction. Without this force the plant may reproduce itself by non-sexual means, by vegetative processes such as the formation of runners, suckers, etc. Under the influence of this force it will multiply only by sexual means. In such a case, the one force would control reproduction, both sexual and non-sexual. The effect of the force as a controlling agent is due to its own direct influence upon the plant and also to the irritable response of the plant to its influence, the response setting in motion other forces in its own body. The force from without is but the initial energy which releases other quantities of energy, thus setting in operation other processes than those which it can directly affect.

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* Klebs, G. Zur Physiologie der Fortpflanzung einiger Pilze. Jahrb. f. wiss. Bot., pp. 146-7. Bd. 35, 1900.

† Vöchting, H. Über den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. Jahrb. f. wiss. Bot.. Bd. 25, 1893.

Of the many plants studied by Vöchting, *Mimulus Tilingi* serves best to illustrate the facts which he has brought out. Figures 22 and 23 in the accompanying illustration indicate the normal habit of potted plants of this species, respectively a blooming and vigorous plant from a last year's cutting, and a much younger one not yet ready to bloom. The vegetative functions, as well as the vegetative mode of reproduction, of the plant, are carried out by the usually more or less creeping leafy branches originating on the stem just above the surface of the soil. When the vegetating period draws toward the close, the new internodes of these branches are successively shorter, the tips of the branches forming finally rosette-like bunches of leaves on the surface of the soil. Such a bunch cut off and transplanted will presently give rise to the flowering erect branch shown in figure 22. The rosettes will form erect branches, however, only when warm enough. The upper part of an erect branch bears flowers. Just below these are a few pairs of leaves in the axils of which short vegetative branches begin to form. The flowering part of the branch may bear lateral flowering branchlets if the plant is vigorous. After fruiting, the whole branch usually dies to the ground, and then the rosette from which it arose will give rise to the lateral creeping branches by which new rosettes will be formed. Thus non-sexual vegetative reproduction follows the sexual mode, the same plant being capable of both but not of both simultaneously. Before it has flowered, however, a rosette is not likely soon to branch and to form new rosettes.

If vigorous young plants which, under ordinary conditions, would presently bloom are so placed that they have only enough light for active vegetation but otherwise are very favorably situated, they will not form the erect flower-bearing branches, but will continue to grow and will presently form creeping branches, spreading and maintaining themselves in this way. Plants may be kept from blooming by this means for an indefinite length of time. Vöchting reports having kept plants sterile for three years. The effect of such enforced sterility on the health of the plants appears to be neither favorable nor unfavorable. Under otherwise like favorable conditions plants which have not flowered present as vigorous an appearance as those which

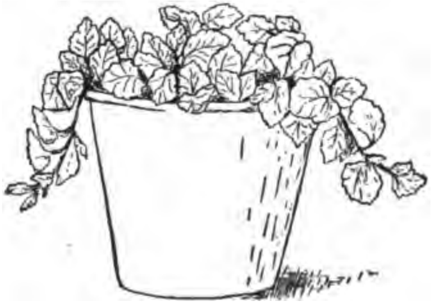

Fig. 23

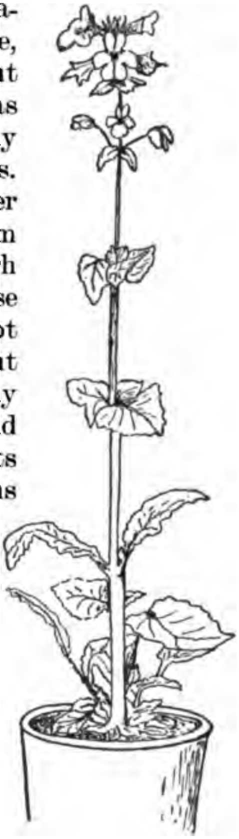

Fig. 22

Figures 22. 23. *Mimulus Tilingi.* Figure 22, a blooming plant from a cutting of the preceding year. Figure 23, a younger plant not yet ready to bloom. (After Vöchting).

have flowered and seeded. In every way they behave alike. It would seem then that these plants require, as the stimulus to form flowering branches, an intensity of light which is more than sufficient to maintain the vegetative activities at a perfectly healthy pitch.

Vöchting further shows that various degrees of illumination above what is sufficient for the vegetative processes, but insufficient for those connected with sexual reproduction, will produce effects exactly corresponding to the degree of illumination. Light enough to induce the formation of an erect branch and its growth to a height of several centimetres may be insufficient to induce the formation of any flower-buds upon it. Still stronger illumination will insure the formation of flower-buds and their attaining a very considerable size, but will not induce them to open. The bearing of this fact on the formation of cleistogamous flowers Vöchting considers very important. Such a degree of illumination, instead of inducing the perfect development and opening of flower-buds, will stimulate the vegetative buds in the axils of the pairs of leaves, just below the flowering part of the erect branch, to develop. Still stronger light, inducing the opening of the flower-buds, if still insufficient, is indicated by the small size of the flowers or by the rudimentary condition of some of the floral organs. The corolla, and in two-lipped flowers the upper lip, give evidence by their imperfect development of slightly insufficient light, while to suppress or to reduce the calyx still less light must fall upon the plant. The essential organs, stamens and pistils, are least dependent upon light. However, the flower as a whole, all of its parts, and even the branch which bears it, are dependent for their formation upon illumination of sufficient intensity and duration.

The light evidently acts as a stimulus, inducing certain effects, for if the formation of a flowering branch has begun, its growth will continue for a time even in darkness. If the formation of flowers on the branch has begun, they too will continue to grow in darkness. But to insure the perfect development of the flowers of most plants, sufficiently intense illumination, repeated with sufficient frequency, is absolutely necessary. In other words, the stimulus is but transient. Repeated stimulation is needed to continue in operation the processes by which the formation, growth, and perfect development of flowers, and their accessory parts, are accomplished. In some few plants, flowers which have been duly induced to form will develop perfectly in the dark, but in most plants abnormal characters will appear, varying in importance from an insufficiency of color to deformity or suppression of parts, or the failure of the flowers to open.

Sachs's hypothesis,* that certain specific substances, presumably made in the leaves under the influence of light, are necessary for the formation of flowers, breaks down under Vöchting's experiments, for we cannot reasonably admit the presence in the plant of corolla-forming material as distinct from calyx-forming, etc.

When a plant is so well nourished, has attained such a size, and is under such favorable conditions generally, that it is able to form the organs and substances of sexual reproduction, it must be that it will do so whenever the processes concerned in sexual reproduction are set and maintained in operation by a stimulus from outside. This stimulus is the light. Without it, the higher plant cannot reproduce, or even prepare to reproduce, itself sexually. The plant is sensitive to that force which, in cases where the plant is dependent upon insects for cross-pollination, will in so far as possible ensure the visits of the necessary insects. It would be interesting to determine whether other than entomophilous flowers are so sensitive to light and so dependent upon it.

The influence of light is to be distinguished from the influences of food, water, and of the other substances, of heat and of the other forces, essential to active life. With insufficient warmth, food, or water, the plant will be imperfectly able, or quite unable, to reproduce itself by sexual means; but this inability is due to the effect of unfavorable conditions upon all of its vital functions. Warmth, food, water, etc., sufficient to ensure the perfect accomplishment of its vegetative functions, will favor the accomplishment of sexual functions also. More than enough warmth, food, water, etc., for these purposes will not act as a stimulus to the plant to engage in the processes preliminary to and composing the sexual functions. The special stimulus of light is necessary, and in this respect light differs from the other forces and from the matters upon which the plant depends and to which it irritably responds.

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* Sachs. J. von. Lectures on the physiology of plants. English Ed.. Oxford 1887. and his special papers therein referred to (pp. 530. 534. etc.)

We are told that Arctic and Alpine flowers are especially brilliant, and in certain parts of the temperate zone the brilliancy of the flowers, their large size, perfection, and number is a matter of local pride and of general admiration. According to the hypothesis of natural selection, Arctic and Alpine plants produce especially fine flowers because, in order to secure cross-pollination from the comparatively few insects of those regions, the flowers must be especially conspicuous; that less conspicuous flowers, less attractive to insects, set fewer or no seed, and that finally the plants which bear them become extinct. This may be the case, but Vöchting's work suggests an explanation more susceptible of experimental test. During the Arctic summer, brief though it is, the hours of darkness are few, the hours of light many, and the light often intense. Alpine regions are like Arctic regions in that the summer is brief and the light intense. Certainly the high mountain side receives more light per hour of clear sunshine than does the valley below, and in clear weather the mountain side is illuminated for more hours per day than is the valley. This factor, light, may therefore play a very important part in connection with the sexual reproduction of plants of high altitudes and latitudes.

One more point should be mentioned before we leave the subject of the influence of light on blooming. Vöchting found that he could convert all the flowers of *Viola odorata* into cleistogamous ones by diminishing the light. He could not, however, by the opposite course, bring about the development of all the flowers into chasmogamous ones.

He quotes Delpino* as saying that in one part of Liguria the plants of *Viola odorata* bear only the open flowers, while near Turin both kinds occur on the same plant. Here in California cleistogamous flowers are few, confined in the main to the forests, the floor of which is but dimly lighted. Is this because of the brilliancy of the sunshine?

What are the advantages of sexual and non-sexual reproduction? Before it began to be shown at all that reproduction, like other functions, exhibits in its course the irritability of the organism, sexual and non-sexual reproduction were compared solely with regard to the species, the offspring, and the conditions in which they would find themselves when separated from the parent. For example, *Vaucheria* produces resting spores by sexual means, immediately germinating zoöspores by non-sexual means. When the conditions are becoming less favorable for active vegetation, and when active vegetation finally becomes impossible, it is obviously to the advantage of the offspring and to the species that the new individuals should be of such character that they can withstand unfavorable influences for a time. But between the advantage of forming resting-spores when the conditions are to be unfavorable, and the means of attaining this desirable end, there would be a great gap had it not been shown that the influence of circumstances upon the parents causes them to form resistant instead of extremely sensitive reproductive bodies. There must be some advantage to the parents, as well as to the offspring, else they would not engage in sexual reproduction. According to circumstances, according to stimuli, according to the advantage of the mature individuals, they will continue to vegetate, or they will form non-sexual spores or vegetatively produced individuals (bulbs, runners, etc.), or they will form new individuals by sexual means. In the orderly succession of events in nature, changes in the water-courses, in the soil, and in the air normally precede a degree of heat, dryness, or cold which suspends active vegetation. These preliminary changes give the stimulus which causes plants to change their behavior accordingly. So, also, changes of other sorts, making the conditions suitable not only for the growth and healthy life of the individual but also for the production and active life of new individuals, will induce plants to form these by sexual or by non-sexual means, according to the species of plant. In the spring, when the conditions for active vegetation are becoming more and more favorable, the *Equisetums* complete the development of the spores non-sexually formed in the foregoing season, and shed these spores, which germinate at once, if at all, and form new plants, the prothalli. These, if conditions favor, soon develop sexual organs and produce new plants by sexual means. In these alternating generations, the non-sexual and the sexual, which follow one another in successive years, the conditions of the later growing period of one year induce the mature plants to form spores by non-sexual means. The different conditions of the earliest growing period of the following year induce the same plants to complete the development of the spores already formed. The still different conditions of the days and weeks succeeding induce these spores to germinate, the prothalli to form archegonia and antheridia, the embryos to develop into the larger non-sexual plants. These last vegetate for an indefinite length of time. The successive changes in the seasons, in the soil, and in the water-supply, fix the succession of generations which recur according to the peculiar adjustment of the species to all the factors of its environment. Species, genera, families, and orders differ in their adjustments and in their reactions to the stimuli given by the many different factors composing the environment.

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* **Delpino, F. Sull' Opera, la Distribuzione dei Sessi nelle Piante etc., 1867.**

Comparing sexual and non-sexual reproduction, we see that the advantage of the parents determines what mode of reproduction, if any, shall be carried out. For a long time it has been supposed that sexual reproduction is distinctly advantageous to the species, if not occasionally altogether necessary to those forms capable of reproducing themselves by this means. Such a view is not quite correct. Many species of plants, among them forms which are eminently successful as judged by their numbers and activity, are wholly incapable of reproducing themselves by sexual means. The bacteria, the higher fungi, and many independent plants illustrate this. Some of the higher algæ, archegoniates, and flowering plants may go on indefinitely, without reproducing themselves by other than purely vegetative means, and with no evidence of injury to the individual or to the species. It is only when special conditions produce special effects on plants, that they need to reproduce themselves by sexual or non-sexual spores. Under special conditions, reproduction becomes a necessity by becoming advantageous to the individual. The species profits accordingly.

Certain advantages to the species are conceivable in the spore method of reproduction over any vegetative method, and certain advantages are conceivable in the sexually produced offspring over those non-sexually produced, but these are conceptions rather than proved facts in all but a very few cases. These few cases may or may not be typical of the majority. It is conceivable, for example, that the formation of new individuals by runners, as in the strawberry, and by suckers, as in the coast red-wood (*Sequoia sempervirens*), is advantageous to the species. The new individuals hold the territory won by their parents and may even extend it somewhat. The young are nourished by the parent until they have attained size, strength, and development which give them an advantage in competing with other plants for space and for the means of existence. These means of reproduction are, however, defective in that they do not secure the dispersal of the new individuals and consequently do not tend to insure the survival of the species or to extend its territory rapidly enough. The survival of the well-equipped offspring formed by vegetative means is certain so long as the conditions in the space occupied by the parent remain favorable, but such reproduction is dangerous, because wide dispersal will secure for the species some positions at least in which it can be maintained whatever may befall individuals in other places. A puddle may become densely populated through the vegetative reproduction of the algæ and animals started therein, but unless these give rise to spore or other resting stages all the species will be locally destroyed when the puddle dries. Vegetative reproduction is in many cases the most effective means of multiplying the number of individuals, but it is seldom effective in securing wide dispersal or in insuring the permanence of the species. These two needs are generally met by the formation of non-sexual or sexual spores and their products (seeds, fruits). The non-sexually formed spores of the ferns, and archegoniates generally, and of the lower plants, fungi and algæ, are especially adapted by their small size and in various special ways to secure wide dispersal. They may or may not be very resistant. According to the plant which forms them, and according to the season at which they are formed, they will be resting-spores or such as must germinate at once if at all.

New individuals vegetatively produced, and those from germinating non-sexual spores, will contain material from their single parent only. By sexual means, there are united in the offspring substances from both parents. Among the lowest plants (and animals) the visible differences between the two parents are only slight. In higher plants, however, where the new individuals are formed by the fusion of sexual elements themselves obviously unlike, formed in organs and by parents also obviously unlike, it is evident that a new balance of forces and matters may be, but not necessarily will be, possessed by the offspring. Maternal and paternal characters may offset or intensify one another; maternal influences during the development of the spore or embryo may or may not neutralize the paternal influence carried into the germ-cell by the sperm. The offspring sexually produced, representing a new adjustment, may be better adapted to prevailing conditions than was either parent. These are all possibilities, seldom probabilities, almost never certainties. The chances are even that the offspring will be like the average of the species. Some may be worse, a few may be better, but unless the better, when it comes their turn to reproduce sexually, mate with others equally good, their offspring will almost certainly be like the average of the species. The statistical study of variation,* now so much the fashion among biologists, shows how wide the range of variation is. The inevitable result of combining two different things is the production of a mean or balance. In this balancing or equalizing (*Ausgleich*), Strasburger† sees the essential character of sexual reproduction and its fundamental advantage over all other modes of reproduction.

In certain species sexual reproduction seems to be absolutely necessary to escape degeneration and extinction. This has been shown to be the case among certain *Infusoria* and Diatoms, but these are special cases in which the individuals by prolonged division (vegetative reproduction), incompletely offset by growth, have become unduly small and weak. By the fusion of two such individuals the normal amount of substance and the normal means of securing energy are furnished to the new individuals. Except in these special cases, and in the highest animals, sexual reproduction does not seem to be necessary to the maintenance of the species in a healthy condition, in which it stands a good chance to succeed in the struggle for existence.

HEREDITY

The physiologist is confronted with the problem of heredity. He sees plants resembling one another in succeeding generations and he hears discussions of the means by which the characters and the tendencies of the parents are transmitted to the offspring. What is "heredity," and what are the means by which the offspring are made to possess the characters and tendencies of their parents? "Heredity is the biological law by which living beings tend to repeat their characteristics in their descendants."‡ The means are of two sorts—*first*, the continuity of substance from parent to offspring, and *second*, the continuity of influences to which organisms are exposed. These means are continually emphasized and for the most part ignored, respectively. The former are for morphology to describe, the latter are within the province of physiology to discuss. Granting the continuity of substance, which we have already considered (pp. 255–63), what are the influences which are continuous?

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* Shull, G. H. A quantitative study of variation in bracts, rays, and disk florets of Aster Shortii etc. Amer. Naturalist, vol. 36, 1902.

† Strasburger. E. Über Befruchtung. Bot. Zeitung, 1901.

‡ See Ritter, W. E. The power and methods of heredity. University Chronicle, vol. III., Berkeley. Cal. 1900.

The environment of an organism is made up of many factors, some great, some small, as judged by their visible effects, some continuous, some constant, some variable, some occasional, some periodic. Among continuous factors the following may be mentioned. *First*, the atmosphere, the composition and pressure of which are unchanging. *Second*, water, which has the same composition, the same solvent power, and the same carrying power always. *Third*, gravity, a force of uniform strength. *Fourth*, the earth as a whole, the character of which changes only with inconceivable slowness. If these factors are not absolutely continuous, taking infinite time into account, they are continuous and unchanging so far as millions of generations of organisms are concerned. They are exactly the same for the offspring as for its parents.

On the other hand, light and heat are forces which act periodically with great regularity, but which are constant only within rather wide limits. Of the influences which are occasional, other and motile living organisms are perhaps the most striking.

The continuous and the periodic influences are the ones which have received least attention from those interested in the problem of heredity. These influences must conserve if the variable and occasional influences introduce differences. But as a basis for all conceptions of heredity and variation, we must concede the irritability of living protoplasm.

The egg, which is a part of the living substance of the mother, is penetrated by the spermatozoid, a part of the living substance of the father, and these two fuse into one mass of living substance. Each particle of living substance, while still within the body of the parent, was influenced by all the forces, constant and otherwise, which were then operating. Assuming the irritability of living protoplasm, any force which influences it will set up a reaction of some sort in it, though this reaction may not be visible at the time. Between the time of leaving the parent and meeting and fusing with its mate, each sexual element was influenced by and reacted to all the forces then operating. By the fusion of these two living masses into one, the resultant effects of all preceding influences upon the two separate masses are united. From the moment of fusion, the single mass is influenced by all the forces and matters, continuous, constant, and variable, which constitute its environment. If the fertilized egg remain within the body of the parent, it is subjected, during the period of gestation, to mechanical and other influences, some of which absolutely limit it in form and size. For instance, the young zygospore of *Spirogyra*, the young oöspore of *Œdogonium*, the fœtal colt, in the body of the mother, are limited as to form and size by the enclosing walls of cell or uterus. They could not grow beyond a certain size, though they may never reach this size, because growth would be mechanically hindered and stopped by the surrounding cell or uterine walls. In form also they are similarly limited, not as the mould fixes the size and shape of the cast, but because, by excessive growth in one direction or part, they would encounter the mechanical resistance of the enclosing walls of cell or uterus.

The young and forming individual, whether one-celled spore or many-celled embryo, is affected also by food, warmth, position with relation to gravity, etc. Of these influences, we know least about the most constant. The most constant influences have so far baffled the experimenter to eliminate. Since they are the most difficult to eliminate, it is reasonable to conclude that they are also the most powerful. If they oppose the experimenter, they must also affect the young and forming individual.

If the fertilized egg is not enclosed within the body of the mother, it too is subjected to all the influences composing its environment, to influences which have changed with inconceivable slowness if at all, as well as to changing influences.

The dominant power of the unchanging influences is shown by man's inability to make fundamental changes in living organisms by experiment, and by the absence of any proof of the so-called "inheritance of acquired characters." If man could eliminate the force of gravity in experimenting on an organism, he might obtain other results than now, when all he can do is to expose the organism on all sides to the force, or to oppose gravity by centrifugal or other force. If he could change the composition of water, or find a substitute for it, he might make some fundamental change in the organism under experiment. He cannot remove the air from around a plant or animal without at once changing the conditions of his experiment in other ways also, and the result of such experiment is of little value in the subject under discussion, because it is produced by a combination of changes.

We may safely conclude, then, that the unchanging factors in its environment, to which it irritably responds, are among the most powerful, if they are not the only, influences which make the offspring like its parents. The changing factors cause it to vary. Heredity is possible only because of the irritability and continuity of living protoplasm, and the continuity of certain influences acting upon this.

Heredity is a mystery, but so is the form of a crystal of common salt. *Spirogyra* plants are no more and no less alike than are crystals of common salt. Does common salt "inherit" its crystalline form? Crystals of common salt represent the reaction of NaCl molecules to their environment, of which some factors are constant and others changing. *Spirogyra* cells represent the reaction of the molecules and combination of molecules of which its living protoplasm consists, to their environment, of which some factors are constant and others changing. Given the continuity of the irritable substance (protoplasm) from parent to offspring, heredity and variation are the inevitable results of the constant and of the changing factors respectively, which, taken together, compose the environment. These influences at least we can more or less definitely study in their relations to heredity. Though there doubtless are other factors contributing to heredity, they are not yet included within the domain of physiology and need not be discussed here.

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